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THE TIME OF APPEARANCE OF OSSIFICATION CENTRES IN THE PEPPIN-TYPE MERINO

By A. K. Lascelles*

[*Manuscript received December* 22, 1958]

Summary

The time of appearance of appendicular ossification centres in the Peppin-type Merino foetus has been established using radiological methods on 68 foetuses of known age. A standard of reference of the aging process or maturation process of bone has been drawn up using the number of ossification centres present and the contour changes of certain of these centres as a yardstick. Osseous maturation is thus given a numerical score. Measurements of tibial and body length have also been taken. The entire data (the four variables being age, body length, tibial length, and osseous maturation score) have been subjected to a correlation analysis. Very high correlation coefficients were obtained, ranging from +0·98 to +0·99. It is thus clearly seen from the results of the analysis that body length, tibial length, or osseous maturation measurements are of equal value in assessing the age of the foetus. Furthermore, because of these high correlations a combined regression equation would be pointless.

I. Introduction

Bone development can be conveniently divided into two components—growth and maturation (or differentiation). Growth is a simple characteristic to measure; maturation on the other hand is more elusive to measurement and is difficult of precise definition. It is usually described as the metamorphosis of the cartilagenous and membranous framework of the foetus to the completely ossified bone of the adult. In the normal process of maturation osteoid tissue becomes calcified and hence can be conveniently studied by X-ray techniques.

The maturation process in the appendicular skeleton can be arbitrarily divided into four stages:

(1) The formation of the cartilagenous primordia.

(2) The appearance of primary then secondary centres of ossification, i.e. the replacement of the centres of the primordia by bone.

(3) The expansion and modelling of the osseous centres.

(4) The closure of the epiphyseal lines.

Stages 2, 3, and 4 have been studied extensively in human foetuses and children because it is from these aspects of bone development that information may be drawn to compile tables or standards of progressive maturation. Such knowledge has proved invaluable to clinicians in differentiating certain endocrine disturbances (Engelbach and McMahon 1924; Shelton 1931; Clark 1936; and others).

* Department of Veterinary Medicine, University of Sydney.

The maturation of the skeleton in the sheep has been limited to a few studies on the appearance of ossification centres. Harris (1937) employed both alizarin staining and radiography in the examination of 28 foetuses of known age. Because of the small number of specimens examined, it was impossible to give well-defined limits to the time of appearance of centres. Furthermore, breed and sex of the sheep studied was not given. Benzie (1950) surveyed the development of the skeleton of the Scottish Blackface. His conclusions were based on information derived from radiological examination of 12 foetuses of known age.

Smith (1956) accurately established the order of appearance of appendicular ossification centres using mainly radiological methods of examination. 320 foetuses of unknown age were used in this study and the order given was based on crown–rump length measurements.

The aim of this study has been to establish the time and order of appearance of appendicular ossification centres in the Peppin-type Merino foetus. In addition a simple standard of reference of the osseous maturation process has been drawn up in preparation for studies on hypothyroidism in the foetal sheep of the same strain and breed.

II. Materials and Methods

The 68 foetuses used in this work were collected at the Agricultural Experiment Station, Trangie, N.S.W., following artificial insemination of Peppin-type Merino ewes with semen of rams of the same breed and strain. The ewes were slaughtered at intervals throughout the gestation period and age of the foetuses thus collected was taken as the time since insemination. The body length of the foetus was measured in inches by placing a piece of string along the mid-dorsal surface of the body commencing at a line joining the medial canthi of the eyes and terminating at the tip of the tail. The string was marked at the appropriate point and compared with a fixed scale. This method of measurement was first recommended by Cloete (1939) and recently by Dun (1955) as a means of predicting age.

The material was fixed in formalin and transported to Sydney University. The left fore and hind limbs were carefully dissected from the trunk and were X-rayed, both lateral and dorsal views being taken. The factors used were 45-50 kV, 30 mA, 0·2–0·5 sec at 36 in., being varied in the given ranges according to the size of the specimen. Non-screen X-ray film (Ilford) was used throughout.

The length of the tibial diaphysis was measured by using calipers. The proximal and distal landmarks used for measurement were points situated half way between the anterior and posterior aspects of the bone. The distance was measured in inches to the nearest 0·025 in.

An ossification centre was scored present when distinct evidence of relative opacity in the appropriate area was found. If there was any doubt, the centre was considered absent. Where duplication of a centre of ossification occurred within a limb (such as metacarpals, metatarsals, sesamoids, and digits) the centre was only scored once and further was considered present if only one centre of the pair or group was present. Inconstant centres, i.e. centres which are not present in all individuals, were ignored in this work.

III. Results

One method of presenting all the information on the time of first appearance of centres of ossification in the limited data available was by giving two ages, i.e. the

Table 1

ORDER OF APPEARANCE OF OSSIFICATION CENTRES BASED ON MEAN AGE OF APPEARANCE

Mean Age (days)	Centres
46	Body of scapula; shaft of humerus; shaft of radius; shaft of ulna; shaft of metacarpus; shaft of femur; shaft of tibia
49·5	Shaft of metatarsus
59	Shaft of first phalanx (fore limb)
61	Shaft of first phalanx (hind limb)
64	Shaft of second phalanx (fore limb)
69	Shaft of second phalanx (hind limb)
71	Third phalanx (fore limb); third phalanx (hind limb); calcaneus
79·5	Talus
98	Third carpal, distal; fourth carpal, distal; distal epiphysis of femur; scaphoid
102	Cuboid
104·5	Distal epiphysis of radius; radial carpal; intermediate carpal; ulnar–carpal
106	Second and third tarsal, fused
107	Distal epiphysis of humerus
108·5	Epiphysis of metacarpus and metatarsus
109·5	Proximal epiphysis of tibia
113	Proximal epiphysis of radius
118	Proximal epiphysis of humerus; proximal epiphysis of first phalanx (fore and hind); distal epiphysis of tibia
119	Lateral tuberosity of humerus
121	Proximal epiphysis of second phalanx (fore and hind)
122	Proximal epiphysis of ulna
123	Patella; epiphysis of calcaneus
126	Head of femur
127	Accessory carpal
128	Proximal sesamoids (fore)
129	Tibial tubercle
132	First tarsal, distal; tuber scapulae
133	Distal epiphysis of ulna
136	Lateral malleolus
137	Lateral epicondyle; tibial tubercle
137·5	Second carpal, distal
140	Medial epicondyle of humerus
141	Trochanter major; proximal sesamoids (hind)
144·5	Trochanter minor

age the centre was first observed and the age it was first constantly present (Smith 1956). A mean of the time of appearance was estimated using the mid-range, i.e.

averaging the two ages. Since each estimate was usually based on only two observations, the standard error is then one-half of the range. The mid-range would nevertheless give a closer estimate of the time of first appearance of an individual centre than either of the other ages.

On this basis the order and time of appearance of the appendicular centres of ossification have been compiled (Table 1).

A curve with a distinct plateau in its centre is produced by plotting the number of ossification centres against age in days (Fig. 1). All the primary centres (including the calcaneus) and the talus appear in the first wave of appearance of ossification centres. The remaining round bone and all the epiphyseal centres make their appearance following a pause.

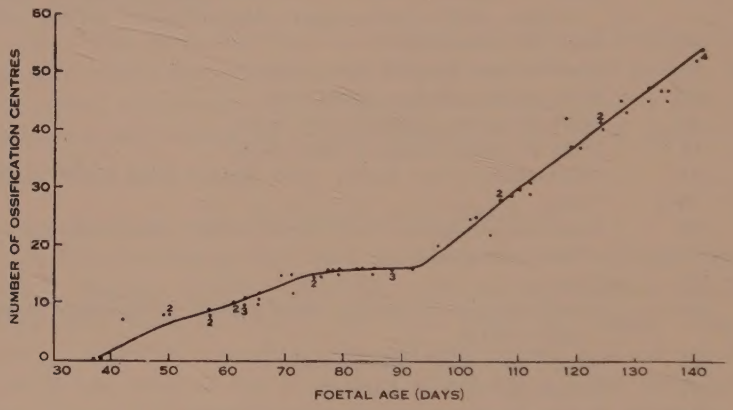


Fig. 1.—Relationship between foetal age and the number of appendicular ossification centres present. In Figures 1, 3, and 4, numerals near graph indicate the number of specimens represented by the nearest marked point. Points without accompanying numerals represent one specimen only.

The Assessment of Foetal Osseous Maturity (bone age)

It had been hoped that osseous maturity assessments would be made simply by counting the ossification centres present in the appendicular skeleton. This method, however, would not apply when attempting to assess osseous maturity during the period of plateau. Thus, for convenience, the foetal period was divided into two sections: 37–92 days and 92–141 days.

In the 37–92-day period the appearance of characteristic contour or shape changes in the calcaneus, talus, and proximal ends of the humerus and femur were allotted a score in units. These anatomical areas were selected because distinct contour changes could be detected easily and further the contours considered were not distorted beyond recognition as a result of slight changes in radiographic projection. The contour changes in these various areas are described and illustrated in Figure 2.

The contour score is then added to the number of centres present to give the total osseous maturity score and when this is plotted against age a linear relation-

ship is found to exist (Fig. 3). The use of the contour changes in bone maturation assessments has been described by earlier workers. Todd (1937) in his studies of osseous maturation in the human sought his criteria of maturation by simple inspection of the shaft ends and in changes in contour of the ossification centres. Acheson (1954) attempted to eliminate subjective error by allotting each specific contour change a numerical score.

The osseous maturity score in the 92–141-day period is assessed by simply counting the number of round bone centres (other than the talus), and the number

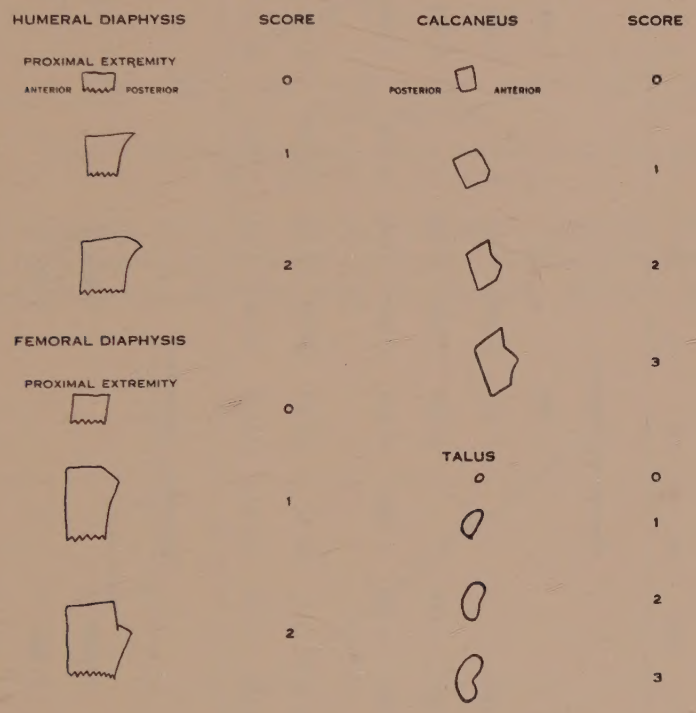


Fig. 2.—*Shaft of humerus:* the proximal extremity of the diaphysis is at first reasonably rectangular in shape until expansion in the posterior direction results in the formation of a spur. A distinct posterior oblique facet is next formed. *Shaft of femur:* the proximal extremity of the diaphysis is initially rectangular, then ossification in the posterior direction results in the formation of an oblique facet. After further remodelling in this region the neck of the femur can be recognized. *Calcaneus:* ossification commences as a round or rectangular centre. An oblique facet is soon visible at the anterodistal corner. The anterior surface becomes curved, i.e. a concavity is formed along its anterior margin. The oblique facet becomes the curved articular suface of the joint between talus and calcaneus. *Talus:* ossification starts as a round, slightly oval centre. The centre in the early stage is symmetrically oval, then flattening occurs along the anterior border. The flattened anterior suface then becomes notched and gradually the notch deepens to assume an appearance somewhat like the mature anterior articular surface.

of epiphyseal centres excepting the lesser trochanter (which is not included in this score because it is difficult to see in most radiographic projections). The osseous maturity score was found to vary linearly with time (Fig. 4).

TABLE 2

CORRELATION MATRICES AND REGRESSION COEFFICIENTS

	37–141-day Period				37–92-day Period				92–141-day Period			
	y	x_1	x_2	x_3	y	x_1	x_2	x_3	y	x_1	x_2	x_3
Correlation Matrices												
Age in days (y)	1·000				1·000				1·000			
Tibial length (x_1)	0·987	1·000			0·977	1·000			0·947	1·000		
Body length (x_2)	0·990	0·993	1·000		0·989	0·982	1·000		0·924	0·970	1·000	
Osseous maturity score (x_3)	0·987	0·991	0·984	1·000	0·968	0·973	0·963	1·000	0·986	0·927	0·927	1·000
$P < 0·001$ if $r >$		0·4				0·5				0·55		
Mean	90·27	62·19	14·6	26·39	67·23	26·43	8·75	13·25	121·27	110·27	22·50	22·19
Standard deviation	30·34	46·32	7·76	18·62	15·23	17·44	3·55	6·94	14·15	24·32	3·97	10·87
Regression Coefficients												
Age in days												
Tibial length (0·025 in.)		0·6505				0·855				0·550		
Body length (in.)		3·896				4·251				3·284		
Osseous maturity score		1·619				2·126				1·283		

The entire data (the four variables being age, body length, tibial length, and osseous maturity score) were subjected to a correlation analysis. For convenience the three periods—37–92 days, 92–141 days, and the total foetal period—have been

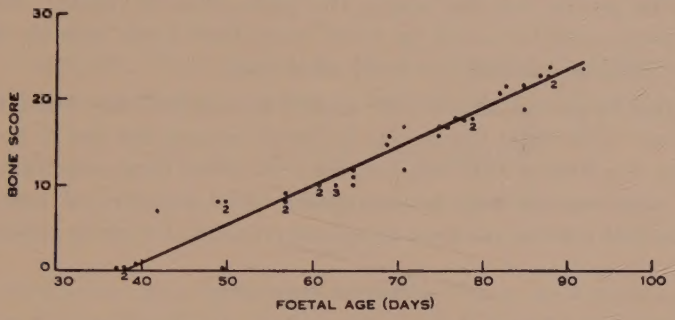


Fig. 3.—Relationship between osseous maturity score (bone score) and age in the 37–92-day period.

analysed separately (Table 2). The high correlation coefficients obtained indicate that any single variable would predict age equally as well as all the variables together. Regression coefficients calculated from the correlation matrices are also set out

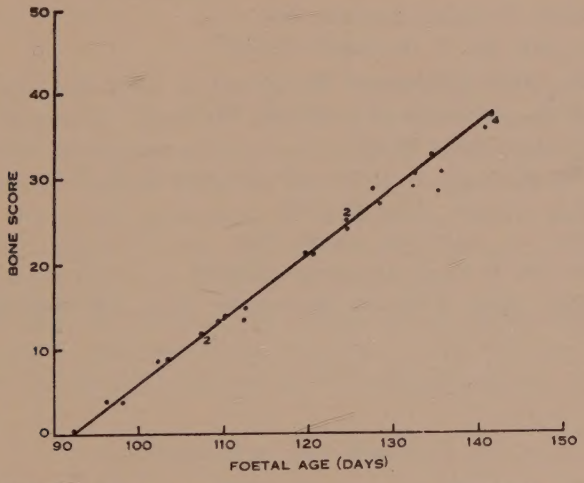


Fig. 4.—Relationship between osseus maturity score (bone score) and age in the 92–141-day period.

in Table 2. The distinctly different slopes of the regression lines of osseous maturity score on age during the first and second sections of the foetal period discouraged the use of a single regression as this would cause heavy bias of age assessment. This argument does not apply as forcefully in the case of age assessments from body and tibial length measurements.

IV. Discussion

The order of appearance of ossification centres established by Smith is slightly different from that presented in the present study. Smith found that the primary

centres of the scapula and femur appeared after the primary centres of the long bones. A perplexing difference was seen in the appearance of the phalanges; in the present study the third phalanx was observed to appear after the second phalanx and the reverse was the case in the order given by Smith. These different findings probably could be solved by more exact techniques, namely silver nitrate impregnation, alizarin staining, or serial sectioning.

Aging the foetus by any of the described methods has been shown to be equally efficient. The tibial length was included because the age of a decomposing foetus is often required in field experiments and under these conditions the simple body-length measurement may be unsuitable. The standard of reference of the osseous maturation process has been presented primarily for use in endocrine studies.

V. Acknowledgments

Grateful acknowledgment is made to Messrs. R. B. Dun and A. Morant, Agricultural Experiment Station, Trangie, N.S.W., for obtaining the foetuses of known age. Thanks are due to Dr. P. J. Claringbold for his statistical advice. This work was supported by a grant from the Wool Research Committee.

VI. References

Acheson, R. M. (1954).—*J. Anat., Lond.* **88**: 498.

Benzie, D. (1950).—*Brit. Vet. J.* **106**: 231.

Clark, D. M. (1936).—*Amer. J. Roentgenol.* **35**: 752.

Cloete J. H. L. (1939).—*Onderstepoort J. Vet. Sci.* **13**: 2.

Dun, R. B. (1955).—*Aust. Vet. J.* **31**:153.

Engelbach, W., and McMahon, A. (1924).—*Endocrinology* **8**: 1.

Harris, H. A. (1937).—*J. Anat., Lond.* **71**: 516.

Shelton, E. K. (1931).—*J. Amer. Med. Ass.* **96**: 759.

Smith, R. N. (1956).—Ph. D. Thesis, University of Bristol.

Todd, T. W. (1937).—"Atlas of Skeletal Maturation." Pt. 1. The hand. (Moseby & Co.: St. Louis, Mo.).

STRONGYLOIDES AND *PARASTRONGYLOIDES* (NEMATODA: RHABDIASOIDEA) IN AUSTRALIAN MARSUPIALS

By M. Josephine Mackerras*

[*Manuscript received January* 20, 1959]

Summary

Strongyloides thylacis, sp. nov. is described from the bandicoot *Thylacis obesulus* (Shaw). It exhibited a regular alternation of generations, similar to that which occurs in many species of the genus.

Parastrongyloides trichosuri, sp. nov. is described from the brush-tailed possum *Trichosurus vulpecula* (Kerr). It also exhibited a regular alternation of generations.

Parastrongyloides peramelis, sp. nov. is described from the bandicoots *Thylacis obesulus* and *Perameles nasuta* Geoffroy. It exhibited an alternation of generations, but homogonic development sometimes occurred as well.

Introduction

Many species belonging to the genus *Strongyloides* Grassi, 1879 have been described from mammals. They are very slender, small worms, which usually live deeply embedded in the mucosa of the small intestine. It seems to be well established that parthenogenetic females occur in the parasitic generation. Their eggs may develop into a free-living generation of rhabditiform males and females, which eventually produce infective larvae (heterogonic development), or they may develop directly into infective larvae (homogonic development).

In 1928, Morgan discovered a very similar parasite in the mole and the shrew in England. However, parasitic males were present, and, on account of this fundamental difference, he erected a new genus, *Parastrongyloides*, for it.

Materials and Methods

The parasitic adults were obtained for study by gently scraping the mucosa of the small intestine with a blunt instrument (the overlying mucus being first removed), and examining the scrapings under a dissecting microscope. This proved a very tedious process, but it was found that naked-eye examination was entirely unreliable, and that it was essential to tease out each fragment in order not to miss these tiny worms.

The free-living generation was obtained by mixing faeces, or contents of the large intestine, with a little sterile water, and spreading the mixture out thinly in a large petri dish, the lid of which was lined with moist filter paper. This process is termed coproculture.

*Queensland Institute of Medical Research, Brisbane.

The morphology of all stages was observed in living as well as fixed material. Permanent preparations were made by fixing the worms in hot 70 per cent. alcohol, or in hot Bles's fixative (formalin 7, glacial acetic acid 3, 90 per cent. alcohol 90 parts). They were mounted in glycerol jelly, or in an aqueous formol–glycerol medium.* Semipermanent preparations were made in lactophenol. Unless otherwise specified, camera lucida drawings and measurements of adults were made on fixed and mounted (and therefore slightly shrunken) material, whereas larvae were drawn and measured unfixed in tap water, simply being immobilized by gentle heat.

The disposition of the gut was most easily studied in living or recently fixed specimens, because the dark, refractile granules in the intestinal cells quickly lost their distinctive appearance in fixatives.

The gonads were best studied when the worms were mounted in the formol–glycerol medium, the glandular elements picking up the stain first, and standing out clearly for a while.

Strongyloides thylacis, sp. nov.

Host.—Thylacis obesulus (Shaw), the short-nosed bandicoot.†

Location.—Small intestine.

Distribution.—Brisbane, Mt. Glorious, S. Qld.; Innisfail, N. Qld.

Type locality.—Brisbane.

Types.—Holotype female and paratype females in glycerol–alcohol in the collection of the Queensland Museum. A series of free-living males, females, and larvae also deposited there.

Morphology of the Parasitic Females

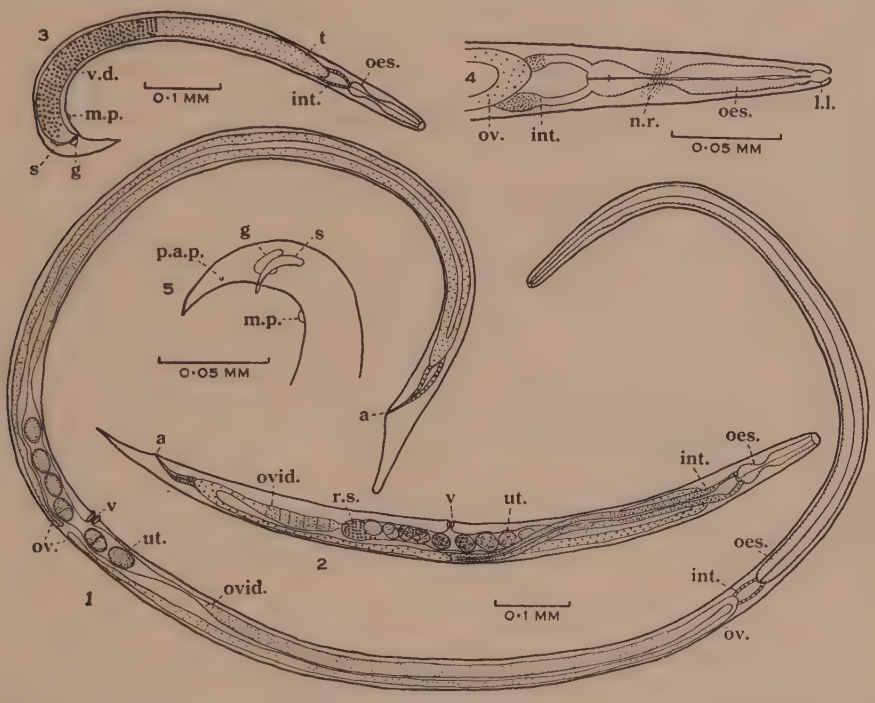
Minute, slender worms, tapering anteriorly. Cuticle with fine rings visible under high magnification. Mouth bounded by minute lips, bearing tiny papillae which are difficult to delineate clearly. Oesophagus divided into a short, narrow, muscular part, followed by a long, wide, glandular part occupying almost the whole width of the body. The ovaries begin dorsally at the level of the vulva: the anterior one passes forwards nearly to the oesophageal–intestinal junction, bends back sharply on itself, and continues as the anterior oviduct, which joins the uterus by a narrow duct; the posterior ovary passes caudally to within about 0·1 mm of the anus, where it bends sharply forward, continuing as the posterior oviduct and uterus. The uteri join, and open immediately at the vulva, a transverse, ventral, slit-like aperture. Tail short, with blunt, finger-like tip (Fig. 1).

*I am indebted to Mr. R. H. Wharton, Institute of Medical Research Field Station, Kuantan, Malaya, for this method, which is superior to the glycerol jelly method for tiny nematodes. The solution consists of 10 per cent. formalin, 5 per cent. glycerol, and a trace of methylene blue in distilled water. Ringing needs to be promptly and carefully done to prevent evaporation.

†Short-nosed bandicoots collected in Queensland conform to the description of *macrourus* (Gould), which is regarded as a synonym of *obesulus*. If, however, they are shown to be distinct species, the parasites recorded here for *obesulus* should be allocated to *macrourus*.

Length 2·25–3·82 mm, average 3·04 mm, by 0·03–0·05 mm in maximum breadth near the vulva. Oesophagus 0·78–0·97 mm in length by 0·028–0·040 mm in maximum width near its posterior end. Vulva 1·45–2·40 mm from the anterior end, average 1·98 mm. Eggs oval, clear-shelled, 0·05 by 0·03 mm, usually laid in the 1- or 2-cell stage. Sperms were never detected in the female ducts.

These worms were most abundant in the duodenum and upper ileum. They were found in almost every bandicoot examined, but were usually present only in small numbers.



Figs. 1–5.—*Strongyloides thylacis*, sp. nov.: 1, parasitic female; 2, free-living female; 3, free-living male; 4, free-living female, anterior end, lateral view; 5, free-living male, posterior end. *a*, Anus; *g*, gubernaculum; *int.*, intestine; *l.l.*, lateral lip; *m.p.*, median papilla; *oes.*, oesophagus; *ov.*, ovary, *ovid.*, oviduct, *p.a.p.*, postanal papilla; *n.r.*, nerve ring; *r.s.*, receptaculum seminis; *s*, spicule; *t*, testis; *ut.*, uterus; *v*, vulva; *v.d.*, vas deferens.

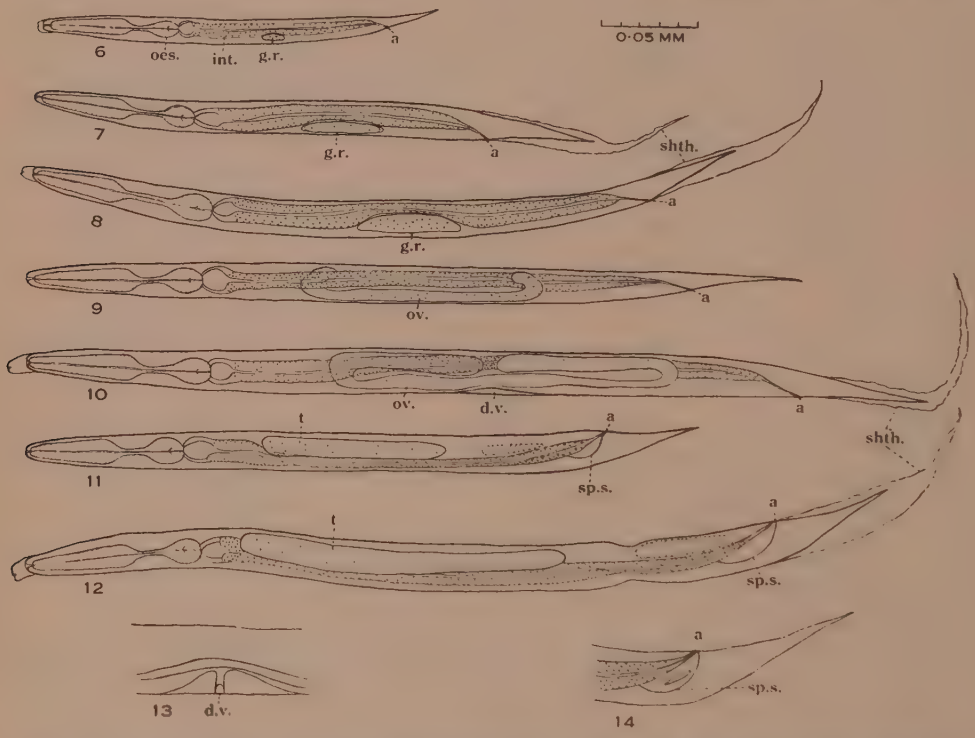
Development of the Free-living Generation

The eggs laid by the parasitic females usually hatched in the intestine, active larvae being found in the faeces.

First-stage larva (*Fig.* 6).—Length 0·20–0·23 mm by 0·015 mm; buccal cavity short; rhabditiform oesophagus 0·07 mm long; tail 0·03 mm long; genital rudiment 0·012–0·018 mm long, lying about the mid-point of the intestine. This stage lasted about 4–6 hr at 28–30°C, the first moult occurring when the larva reached about 0·29 mm in length (Fig. 7).

Second-stage larva (*Fig.* 8).—Closely resembles first stage except in size, the genital rudiment reaching 0·05 mm, and forming a conspicuous object pressing the gut to one side. The second moult occurred when the larva reached about 0·39 by 0·020 mm.

Third-stage larva (*Figs.* 9–12).—During this stage the vestibule loses its long, cylindrical form and becomes cone-shaped. Female larvae may be recognized by the slim tail, and oblique position of the gonad, lying on one side of the intestine in the anterior half of the body and on the opposite side in the posterior half. The ends



Figs. 6–14.—Larval stages of the free-living generation of *S. thylacis*, drawn from unfixed material: 6, first-stage larva; 7, first-stage larva undergoing first moult; 8, second-stage larva undergoing second moult; 9, third-stage female larva; 10, third-stage female larva undergoing third moult; 11, third-stage male larva; 12, third-stage male larva undergoing third moult; 13, fourth-stage female larva, region of developing vulva; 14, fourth-stage male larva, posterior end. *a*, Anus; *d.v.*, developing vulva; *g.r.*, genital rudiment; *int.*, intestine; *oes.*, oesophagus; *ov.*, ovary; *shth.*, sheath; *sp. s.*, spicule sac; *t*, testis.

of the female gonad become reflexed, and the cuticle of the ventral body wall thickened opposite the centre of the gonad. In the male, a pyriform swelling appears in the dorsal wall of the rectum, giving the tail a plump appearance; the gonad remains straight. Female larvae entered the third moult when they were about 0·50 by 0·025 mm, males when they were 0·47 by 0·025 mm.

Fourth-stage larva.—The mouthparts resemble those of the adult. In the female, a depression appears in the vulval thickening (Fig. 13), and the ends of the

reflexed ovaries reach the level of the future vulva. In the male, the spicules gradually take shape (Fig. 14). The fourth moult took place when females measured 0·80–0·90 mm, and males 0·58–0·78 mm in length. The beginning of this moult was observed at 23–29°C, 20 hr after the faeces were passed.

Morphology of the Free-living Adults

Minute, relatively plump worms, with pointed tails. Mouth bounded by two lateral lips each with two tiny papillae. Oesophagus rhabditiform (Fig. 4).

Male (*Fig.* 3).—Length 0·75–0·98 mm by 0·04 mm in breadth. Oesophagus 0·12 mm in total length; corpus 0·06 mm, isthmus 0·025 mm, and bulb 0·035 mm; width of bulb 0·02 mm. Intestine almost straight, usually lying on the left side of the body. Gonad a wide, straight organ; testis beginning close to the oesophageal–intestinal junction; there is a clear line of demarcation between the germinal cells and the mass of sperms stored in the vas deferens. Spermatozoa spherical, 0·008–0·012 mm in diameter. Spicules equal, slightly curved rods, 0·03 mm long, with proximal knobs and rather square-cut tips. Gubernaculum a delicate, curved, shovel-shaped plate, 0·015 by 0·010 mm. Tail slightly curved ventrally, ending in a fine point 0·08 mm from cloaca; unpaired, dome-shaped, median papilla 0·03 mm in front of cloaca; a pair of postanal, ventrolateral papillae about 0·015 mm from cloaca (Fig. 5).

Female (*Fig.* 2).—Length 0·90–1·28 mm by 0·05–0·08 mm in breadth. Oesophagus as in the male. Intestine ventral and to the left of the gonad in the anterior half of the body, swinging over to the dorsal and right side in the region of the vulva, and passing between the ends of the ovaries. Tail sharply pointed, 0·10 mm from the anus. Genitalia essentially similar to those described for the parasitic female, except for the development of a receptaculum seminis at the junction of each oviduct and uterus.

Each ovary begins as a broad, swollen portion lying about the level of the vulva. The anterior ovary passes forward, makes a sharp, U-shaped bend just behind the oesophageal–intestinal junction, and continues as the anterior oviduct. This is a wide tube ending in a short, very narrow duct, which opens into the receptaculum seminis, a wide, sac-like extension of the uterus which only becomes evident when full of sperms. The posterior ovary passes caudally to within a short distance of the anus, bends forward sharply, and its remaining portion is exactly similar to the anterior gonad. The two uteri join and open at the vulva, a transverse, ventral slit lying near the mid-point of the body.

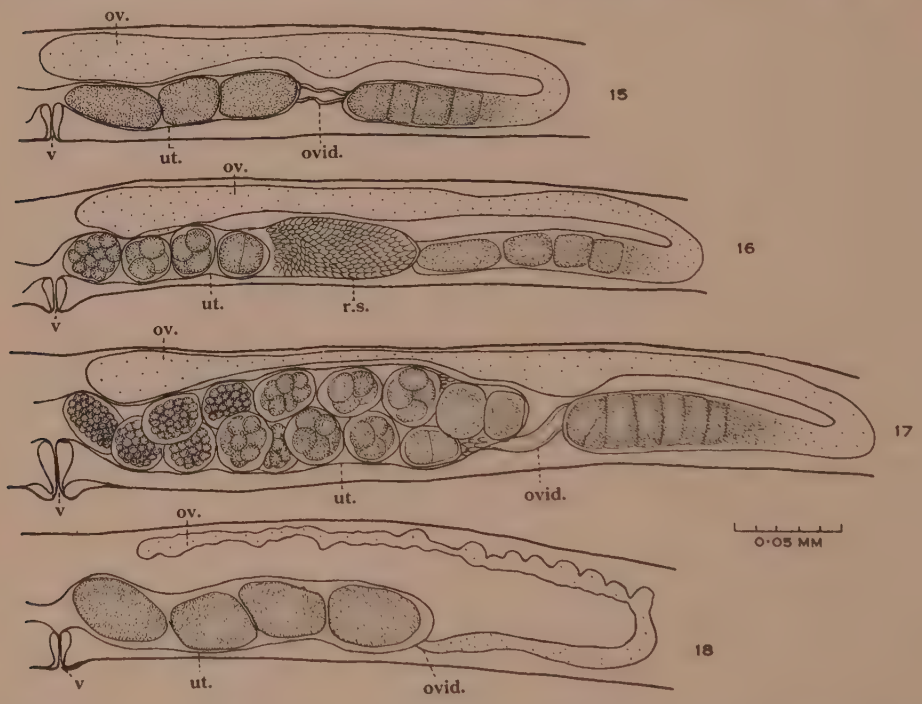
Biology of Free-living Generation

The intestinal cells became loaded with food granules, appearing black with transmitted light and white with reflected light. The portion of the intestine immediately behind the oesophagus (cardia) was usually distended, and its cells remained clear.

Copulation took place with the male at right angles to the female, encircling her body with about one and a half turns. On introduction into the female ducts,

the spermatozoa congregated in the two receptacula and adhered to their walls, remaining stationary when the worm rolled about. They then appeared rather like cubical epithelial cells, with clear bases and rounded, protruding, granular apices.

Ova formed in the oviducts were observed to be squeezed along the narrow duct in a thin stream, each distinctly enclosed in a clear membrane. Upon reaching the receptaculum, each assumed its normal rounded form. If copulation had taken place and the receptacula contained sperms, the ova were quickly fertilized. The entrance of the sperm was not observed, but considerable agitation of the granular mass of the ovum was clearly seen, and segmentation soon began. A double row of developing ova was often seen in females in full egg-bearing (Fig. 17). The eggs were



Figs. 15–18.—Successive appearances of posterior gonad of free-living female of *S. thylacis* seen from left side, drawn from unfixed material: 15, unfertilized, about 20 hr old; 16, shortly after fertilization, about 24 hr old; 17, full egg-bearing, about 36 hr old; 18, spent female at end of third day. Lettering as in Figures 1–5.

often laid in little spurts, several being extruded in quick succession, but they did not adhere to one another in any way. Sometimes eggs in very early stages of segmentation were laid, but there was no regularity about it. Eggs were often retained for longer periods in older females, sometimes until embryonated, and they have been observed to hatch within the uteri in almost moribund females.

The life span of the free-living generation is extremely short, spent and dying adults being observed even on the third day. Some of the females had used up all the sperms, but others still contained sperms after egg production had ceased.

The appearance of the female gonad at successive stages in its evolution is shown in Figures 15–18. In Figure 15, the gonad is shown prior to fertilization. Ova have begun to pass into the uteri, but they are unfertilized and not segmenting; the ovary is a firm, prominent structure. Figure 16 is a drawing made shortly after fertilization; the receptaculum is distended with sperms, and fertilization and segmentation are in progress; receptaculum and uterus are so distended that the narrow oviduct is obscured. Figure 17 shows a female in full egg-bearing. Figure 18 is from a spent female, in which all sperms had been used up, and egg production had ceased; the few ova in the uterus were not segmenting, and the ovary was reduced to an irregular, shrivelled cord of cells.

When young females were separated from males before fertilization, ova continued to form and pass into the uteri, but no segmentation took place.

Development of Infective Larvae

The progeny of the free-living adults developed either into a second free-living generation or into infective filariform larvae. The larvae destined to form free-living adults could be recognized early, because the genital rudiment, which was about 0·010 mm long on hatching, increased rapidly in size, whereas it did not grow at all in those which were destined to become filariforms. The development of the second free-living generation was essentially similar to that already described for the first generation, so the present account will be confined to the development of filariform larvae.

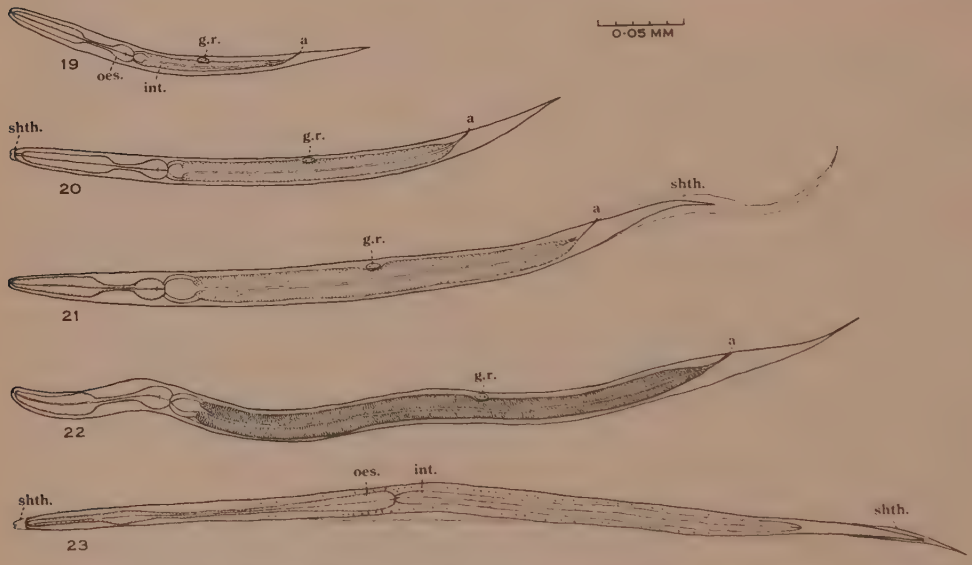
The clear-shelled eggs laid by the free-living females measure 0·040–0·045 mm by 0·038–0·040 mm, being rounder than those of the parasitic females. The shape and dimensions vary slightly, owing to the position of the developing larva. Segmentation proceeded very rapidly on the laboratory bench at 28–30°C on a summer day, and hatching actually began within 4 hr of laying, though it was not complete for 6 or more hours.

First-stage larva (*Figs.* 19 *and* 20).—Newly hatched larvae measure about 0·22 by 0·014 mm. The oesophagus is rhabditiform, and the tail long and pointed. This stage lasts considerably longer than the corresponding stage of the free-living line. The intestinal cells become loaded with food material, and the larva increases in size until it reaches 0·34–0·40 mm by 0·02 mm. The first moult occurred approximately 24 hr after the eggs were laid (Fig. 21).

Second-stage larva (*Fig.* 22).—This resembles the first stage in conformation. The oesophagus is rhabditiform, and the tail long and pointed. The larva grows to 0·50–0·55 mm in length by 0·02 mm in breadth, the oesophagus reaches 0·11 mm in length, and the unchanged genital rudiment lies about 0·3 mm from the anterior end. This is a strong, very active larva with a conspicuous, dark intestine contrasting with the short, pale oesophagus. When the second moult begins, the larva lies stretched out stiffly in a straight line, but is easily stimulated into activity. The oesophagus becomes very hazy in outline as its re-organization proceeds. This is a slow moult, requiring several hours, whereas the first moult is very rapid, and difficult to observe.

Third-stage larva (*Fig.* 23).—The larva gradually becomes slimmer and the tail shorter, and the third-stage, infective, filariform larva can be seen lying within its sheath as the cuticle separates completely. The average length is 0·5 mm by about 0·016 mm in width. The cuticle is finely ringed. In a larva of average length, the oesophagus measures 0·23 mm in length. It consists still of three parts, which are reminiscent of the rhabditiform organ of the preceding stage, but much more elongate, and not sharply marked off from one another. The first part forms about one-third of the total length, and ends in a slight swelling, then follows an extremely slender part, which merges gradually into the wider posterior part—the forerunner of the wide, glandular oesophagus of the adult. The tail is bifid.

This stage sometimes remained within the cast skin for a considerable time, and was capable of intense activity while it was thus ensheathed. Eventually,



Figs. 19–23.—Free-living larval stages of the parasitic generation of *S. thylacis* found in culture, drawn from unfixed material: 19, newly hatched first-stage larva; 20, first-stage larva at beginning of first moult; 21, end of first moult; 22, full-grown, second-stage larva; 23, third-stage (filariform) larva lying within sheath (ventral view). Lettering as in Figures 6–14.

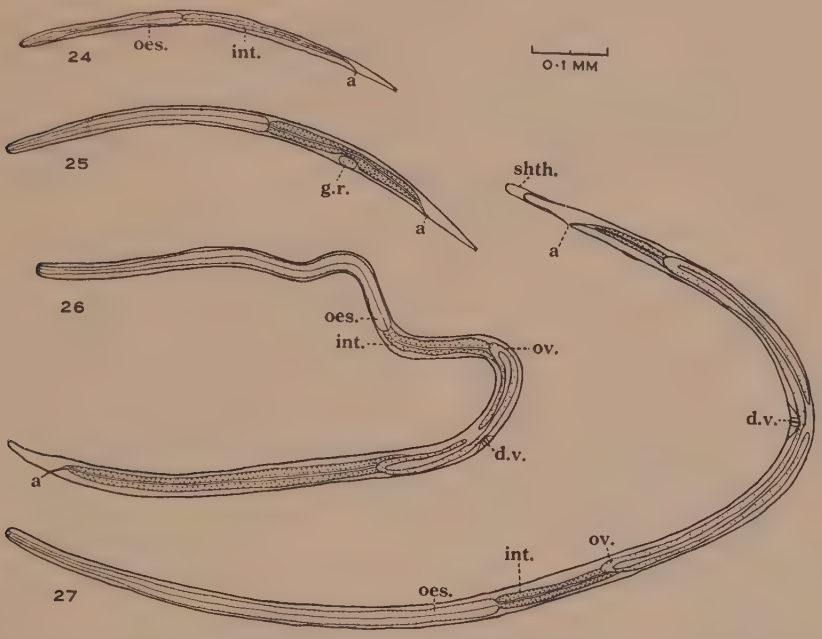
however, the sheath was shed. This long, slim larva moved about with characteristic, rapid undulations of the body. It could climb up the sides of a petri dish, provided they were wet, and was collected in numbers from the moist filter paper lining the lids of dishes used for faecal cultures. Filariforms have been found to persist for at least 4 weeks in culture media which were not too rich nor overgrown with bacteria or fungi.

Development in the Vertebrate

Bandicoots brought into the laboratory were difficult to re-infect, but one young animal, reared in captivity from the pouch, proved to be more susceptible, although it was already naturally infected. Filariform larvae applied to the wetted

skin set up considerable irritation, causing the animal to lick and scratch at the place. Two weeks later, its faeces were teeming with first-stage larvae. However, the infection quickly diminished, only a few larvae being present in the faeces 4 weeks after the artificial infestation. Further efforts to boost up the infection by applying more filariforms failed to make any impression on the degree of infection.

Results with other bandicoots were extremely disappointing. Several adults and one juvenile were re-infected with numerous filariform larvae, and killed after intervals of 1–10 days. None of these animals showed any reaction at the time of application. At 24 hr, one filariform was found in the lungs, but had not increased in size (Fig. 24). At 6 days, two large, third-stage larvae of approximately equal



Figs. 24–27.—Larval stages of the parasitic generation of *S. thylacis* found in the bandicoot, drawn from unfixed material: 24, third-stage (filariform) larva from lung; 25, growing third-stage larva from small intestine; 26, fourth-stage female larva from small intestine; 27, fourth-stage female larva undergoing fourth moult in the small intestine. Lettering as in earlier figures.

size were taken from the ileum. They had the following dimensions: length 0·69 mm, breadth 0·026 mm, oesophagus 0·36 mm, tail 0·075 mm; the genital rudiment measured 0·025 mm; the tip of the tail was bifid (Fig. 25). In the same animal, fourth-stage female larvae measured 1·450 by 0·035 mm, the oesophagus was 0·52 mm long, and the vulva lay 0·83 mm from the anterior end; the tail ended in a minute spur (Fig. 26). Two fourth-stage female larvae were found in the process of the fourth moult. One measured 1·76 mm in length by 0·04 mm in breadth; the oesophagus was 0·7 mm, the vulva lay 1·32 mm from the anterior end, and the ovaries were reflexed and almost reached the level of the vulva. The other specimen was slightly smaller (Fig. 27).

Several unsuccessful attempts were made to infect laboratory rodents. No infection could be demonstrated in eight young rats after oral, percutaneous, or subcutaneous infection with large numbers of filariform larvae. Four young mice were also refractory to percutaneous infection with large numbers of filariform larvae.

S. thylacis is the first member of the genus to be described from an Australian marsupial, but a species is known to occur in the stomach of kangaroos (Winter 1958).

Parastrongyloides trichosuri, sp. nov.

Host.—*Trichosurus vulpecula* (Kerr), the brush-tailed possum.

Location.—Small intestine.

Distribution.—D'Aguilar, Camp Mt., Brisbane, all in S. Qld.

Type locality.—Brisbane.

Types.—Holotype male, allotype female, and paratype males and females in glycerol–alcohol in the collection of the Queensland Museum. A series of free-living males, females, and larvae also deposited there.

Morphology of the Parasitic Adults

Slender, delicate worms, tapering anteriorly; females otherwise nearly uniform in width, but males thickest posteriorly, where the body is thrown into two fairly tight coils. Cuticle finely ringed. Buccal cavity cup-shaped, anterior part of oesophagus narrow and muscular, posterior part wide and glandular.

Male (*Figs.* 29–31).—Length 3·0–4·0 mm, average 3·5 mm, by 0·05–0·06 mm in maximum breadth near the cloaca. Oesophagus 0·73–1·20 mm long; intestine a narrow tube lying at first dorsal and then ventral to the gonad, which is a wide, straight organ, clearly divided into two more or less equal parts, the anterior consisting of germinal tissue, and the posterior, or vas deferens, containing sperms. Spicules strongly curved, with proximal knobs and square-cut distal ends; measuring 0·07–0·08 mm along the curvature, and about 0·05 mm from tip to tip in a straight line. Gubernaculum a delicate, flattish plate. Tail short and blunt; one pair of postanal papillae present, and a small, median, dome-shaped papilla 0·04 mm anterior to the cloaca.

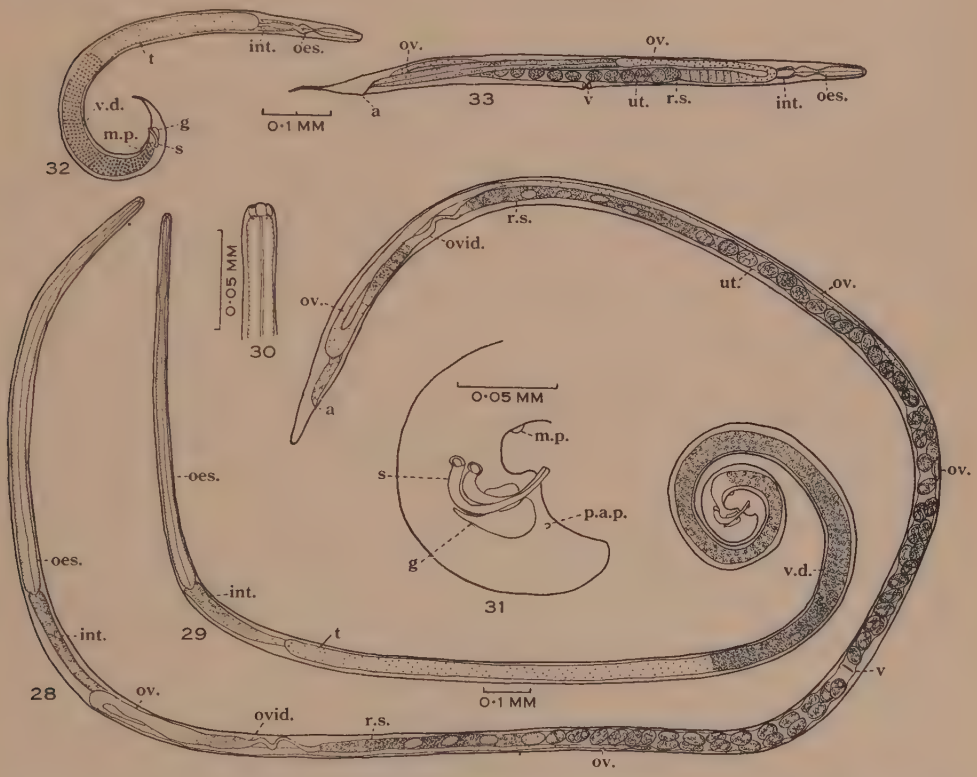
Female (*Fig.* 28).—Length 4·2–5·2 mm, average 4·8 mm, by 0·05–0·08 mm in maximum width near the vulva. Oesophagus 0·9–1·20 mm long. Vulva about 2·8 mm from anterior end, an inconspicuous, transverse, ventral slit. The free end of each ovary lies dorsally about 0·3–0·5 mm from the vulva. The anterior limb passes forwards to within 0·25 mm of the oesophageal–intestinal junction, making a sharp turn, and passing posteriorly again parallel with itself. It merges into the oviduct, which becomes a narrow, rather tortuous tube, opening into the anterior limb of the uterus, just where that organ expands into a receptaculum seminis. The posterior limb of the ovary passes caudally until close to the anus, where it turns sharply forward, and continues as oviduct, etc., exactly as described for the anterior limb. Each uterus a wide tube, opening at the vulva. Uteri of egg-bearing females were crammed with ova in increasing stages of segmentation, those nearest the vulva

being usually in the morula stage, occasionally fully embryonated. Sperms were present in the receptacula seminis and also in the uteri. Tail 0·09 mm, finger-like.

Most of these worms were in the upper part of the ileum, about 150–200 mm from the pylorus. Infection seemed to be common, but usually only a few worms were present.

Development of the Free-living Generation

Parasitic females laid oval, clear-shelled eggs, about 0·055–0·060 mm by 0·035–0·040 mm, usually containing a morula when deposited in the intestine. Freshly passed faeces contained eggs in various stages of development up to fully embryonated, and also newly hatched larvae.



Figs. 28–33.—*Parastrongyloides trichosuri*, sp. nov.: 28, parasitic female; 29, parasitic male; 30, parasitic male, anterior end; 31, parasitic male, posterior end; 32, free-living male; 33, free-living female. Lettering as in Figures 1–5.

First-stage larva.—Length 0·23–0·25 mm by 0·012 mm. Oesophagus rhabditiform. Genital rudiment about 0·015–0·020 mm, lying near the mid-point of intestine. The first moult occurred when the larva reached about 0·3 mm in length.

Second-stage larva.—Similar to first stage, but slightly larger. The second moult occurred when the larva reached about 0·4 mm in length, and was once observed as early as $8\frac{1}{2}$ hr after the faeces were passed (midsummer conditions).

Third-stage larva.—The conformation of the gut resembles that of the previous stages, but immediately after the second moult the sex of the larva can be determined by the reflexing of the ends of the gonad in the female, that of the male remaining straight. The tail of the female is slimmer than that of the male. The third moult occurred when male larvae measured about 0·5 mm, and female larvae about 0·6 mm.

Fourth-stage larva.—The characters of the adult become evident during this stage. A depression appearing in an area of thickened tissue in the female indicates the future vulva. A swelling in the dorsal wall of the rectum in the male contains the developing spicules. Male larvae measured 0·60–0·74 mm, and female larvae 0·70–0·90 mm at the last moult. This was observed between 17 and 18 hr after the faeces were passed, at laboratory temperatures in midsummer and in an incubator at 28°C.

Morphology of the Free-living Adults

Minute, relatively plump worms, with long, sharply pointed tails. Cuticle appearing smooth under low power, but faint rings visible under oil-immersion objective (×1000). Mouth bounded by two well-defined, lateral lips, each bearing two small papillae. Oesophagus rhabditiform; corpus 0·05 mm, isthmus 0·02 mm, bulb 0·02 mm; anterior end of corpus slightly differentiated from remainder. Cardia usually distended, with clear walls; intestinal cells loaded with refractile granules, appearing black with transmitted light and white with reflected light.

Male (*Fig.* 32).—Length 0·64–0·78 mm, average 0·7 mm, by about 0·036 mm in breadth. Intestine lying on left side of body. Spicules equal, slightly curved rods, 0·030–0·035 mm, with small proximal knobs and blunt tips; gubernaculum a delicate, curved plate. A small, median, dome-shaped papilla about 0·04 mm anterior to cloaca; one pair of postanal, ventrolateral papillae. Tail about 0·07 mm, tip slender and flexible.

Female (*Fig.* 33).—Length 0·73–0·86 mm, average 0·8 mm, by about 0·05 mm in breadth. Intestine in left ventrolateral position in the anterior half of the body, swinging over to a right dorsolateral position in the posterior half, passing between the tips of the ovaries at about the level of the vulva. Reproductive organs essentially similar to those of the parasitic generation.

The biology of the free-living generation was essentially similar to that of *S. thylacis*, and the adults were equally short-lived.

Development of the Parasitic Generation

Eggs laid by free-living females usually measured 0·045–0·050 mm by 0·032–0·035 mm, and contained a morula at oviposition. Sometimes nearly spherical eggs were seen, measuring about 0·04 mm in diameter. Old females often laid fully embryonated eggs, or retained the eggs until they hatched *in utero*. Those larvae destined to develop into a second generation of free-living adults followed the course described above for the progeny of the parasitic adults. Those destined to become infective larvae developed as follows:

First-stage larva.—Length 0·24–0·27 mm by about 0·015 mm. Oesophagus rhabditiform. Genital rudiment about 0·010–0·012 mm, lying ventrally near the

mid-point of the intestine. This stage lasted about 22 hr, and the first moult took place when the larva reached about 0·37 mm in length.

Second-stage larva.—Distinguished at once from second-stage larvae of the free-living line by their large size, dark intestine occupying almost the whole width of the larva, and the small genital rudiment, which does not grow appreciably. Second-stage larvae showed great variation in length at the time of the second moult, but the majority measured between 0·5 and 0·6 mm. This moult took a considerable time to complete, the larva lying stretched out stiffly. Third-stage larvae began to appear during the third day of culture.

Third-stage larva.—Length 0·42–0·68 mm, average 0·57 mm, by 0·016 mm. It is essentially similar to that of *S. thylacis*.

Parastrongyloides peramelis, sp. nov.

Hosts.—Thylacis obesulus (Shaw) and *Perameles nasuta* Geoffroy, the short-nosed and long-nosed bandicoots respectively.

Location.—Small intestine.

Distribution.—Brisbane, Mt. Glorious, S. Qld.; Innisfail, N. Qld.

Type locality.—Mt. Glorious.

Types.—Holotype male, allotype female, and paratypes in glycerol–alcohol, in collection of the Queensland Museum.

Morphology of the Parasitic Adults

Minute, slender, delicate worms, thickest in posterior part of body, tapering anteriorly. Anterior part of oesophagus narrow and muscular, posterior part wide and glandular.

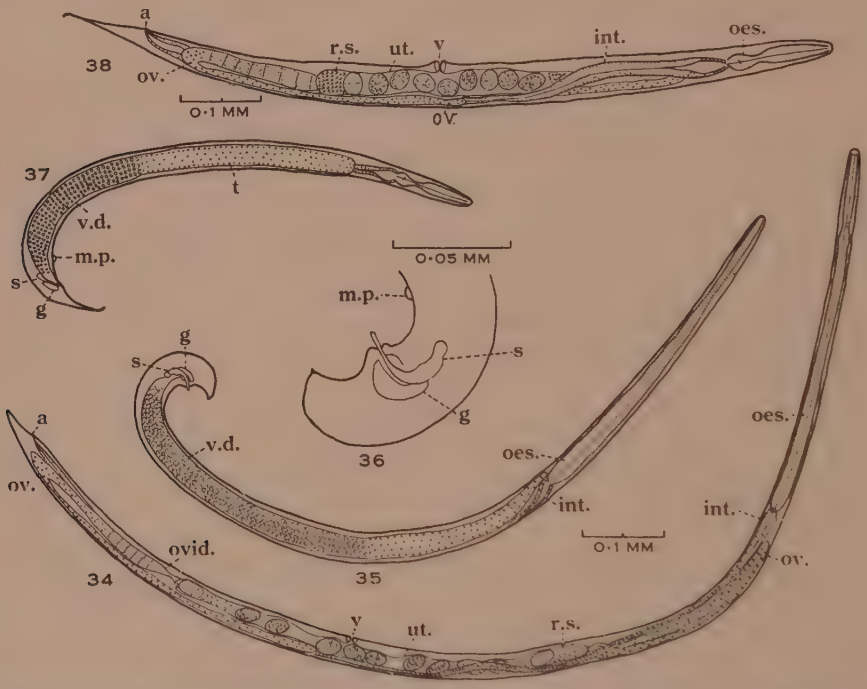
Male (*Figs.* 35 *and* 36).—Length 0·78–1·30 mm, average 1·10 mm, by 0·030–0·045 mm in maximum width near the cloaca. Oesophagus 0·34–0·45 mm long, average 0·39 mm, by 0·025–0·040 mm in maximum width near posterior end. Intestine a thin-walled, straight tube, lying at first dorsal to the gonad, but passing then to the right, and eventually to a ventral position. Testis usually beginning at the level of, or just posterior to, the oesophageal–intestinal junction, and continuing as the vas deferens, the whole gonad forming a wide, straight organ. Spicules equal, sickle-shaped, with knob-like proximal and pointed distal ends clothed in membrane. Each measures from 0·03 to 0·04 mm from tip to tip in a straight line, and about 0·05 mm along the curvature. Gubernaculum a delicate, cradle-shaped plate, 0·020 by 0·017 mm in depth. A small, median, unpaired, dome-shaped papilla 0·04 mm in front of anus, but no caudal papillae detected. Tail bluntly rounded, terminating in a minute, spur-like process.

Female (*Fig.* 34).—Length 1·13–1·98 mm, average 1·6 mm, by 0·03–0·06 mm, average 0·04 mm, in maximum width. Oesophagus 0·38–0·49 mm, average 0·44 mm, by 0·03–0·04 mm in maximum width near posterior end. Intestine a narrow tube lying ventral to the gonad in the anterior half of the body, swinging over between the distal ends of the ovaries to take up a position dorsal to the gonad, and continuing

in this relative position until near the anus. Disposition of the ovaries is very similar to that of *P. trichosuri*, but their free ends lie close to each other at about the level of the vulva. Receptacula seminis and uteri containing numerous spermatozoa. Vulva a transverse, ventral slit lying near the junction of the middle and posterior thirds of the body.

Development of the Free-living Generation

Parasitic females laid oval, clear-shelled eggs, 0·054–0·060 mm by 0·033–0·048 mm. Eggs in various stages of development were found in freshly passed faeces.



Figs. 34–38.—*Parastrongyloides peramelis*, sp. nov.: 34, parasitic female; 35, parasitic male 36, parasitic male, posterior end; 37, free-living male; 38, free-living female. Lettering as in Figures 1–5.

The study of the free-living stages of *P. peramelis* was complicated by the presence of *S. thylacis*. Although some bandicoots had what appeared to be a pure *Strongyloides* infection, no pure *Parastrongyloides* infections were found, except in some preserved material. The development of the free-living generation appeared to be very similar to that of *S. thylacis*, the early larval stages being indistinguishable, but the free-living adults could be differentiated by the appearance of the tail.

Morphology of the Free-living Adults

Minute, relatively plump worms, very similar to *P. trichosuri* and *S. thylacis*. Males measure from 0·67 to 0·85 mm and females from 0·8 to 1·0 mm (Figs. 37 and

38). In both sexes, the tail is slightly longer and narrower than in *S. thylacis*, and is quite frequently kinked, whereas in *S. thylacis* it is more conical and sharply pointed.

Development of the Parasitic Generation

This was essentially similar to that of *P. trichosuri* and *S. thylacis*, but the infective filariform larvae appeared to be larger (average length 0·59 mm) than those of *S. thylacis* (average length 0·5 mm). On two occasions, these large filariform larvae appeared in the first generation, i.e. they had developed directly from the eggs laid by parasitic females.

Incidence of the Infections

Infections in the bandicoots are very common. Thus, during an earlier investigation of lungworms, the faeces of living bandicoots were examined by a modified Baermann technique for metastrongyle larvae. It is some indication of the prevalence of *Strongyloides* or *Parastrongyloides* infections that rhabditiform larvae were recorded in the faeces of 30 out of 31 animals examined in this way.

At a later stage, the small intestines of 13 *T. obesulus* were searched very carefully, with the following results. Nine were infected with *Strongyloides* alone, long females only being found; and four were infected with both *Strongyloides* and *Parastrongyloides*, long and short females being found in all and males in two. A less careful examination was made of nine other animals, autopsied before the occurrence of two species was realized. Of these, two had *Strongyloides* alone, long females only being found, two had a mixed infection of *Strongyloides* and *Parastrongyloides*, long and short females and males being present in both, and five were apparently infected only with *Parastrongyloides*, males and short females being present. These determinations were made on preserved material, and it seems doubtful, in the light of subsequent experience, if they were really pure infections. Indeed, it is probable that more painstaking examinations would have revealed a mixed infection with *Strongyloides* in some at least.

P. trichosuri was found in three out of four possums examined post-mortem, and characteristic larvae and free-living adults were recovered from the faeces of several pet possums.

Discussion

The principal differences between the three species described in this paper are set out in Table 1, the size of the parasitic adults, and the absence of males in *S. thylacis*, being the most useful characters for quick identification. Minute differences only were found between the free-living adults, and none between their larvae, although the infective filariform larvae of *P. peramelis* and *P. trichosuri* tended to be longer than those of *S. thylacis*. The two Australian species of *Parastrongyloides* can be distinguished from the genotype and only other described species, *P. winchesi* Morgan from the European mole and shrew, by the shape of the tail in the parasitic males. It is bluntly rounded, with or without a minute spine, in our species, finger-like in *P. winchesi*.

It is evident from the foregoing that the genera *Strongyloides* and *Parastrongyloides* are not adequately distinguished on morphological grounds—their separation

depends essentially on a biological character, the presence or absence of males in the parasitic generation. The search for these tiny worms must be extremely thorough before it can be said with any confidence that males are absent. However, several careful studies have been made, and it can be accepted that parasitic males do not occur in the species of *Strongyloides* noted below. Thus, Basir (1950) followed every stage in the free-living and parasitic generations of the sheep parasite, *S. papillosus*,

TABLE 1

COMPARISON OF STRONGYLOIDES AND PARASTRONGYLOIDES SPECIES FROM MARSUPIALS

	Strongyloides thylacis	*Parastrongyloides peramelis*	*Parastrongyloides trichosuri*
Host	Bandicoot	Bandicoot	Possum
Parasitic generation			
Males	—	+	+
Length		0·78–1·30 mm	3·0–4·0 mm
Maximum breadth		0·045 mm	0·06 mm
Oesophagus		0·34–0·45 mm	0·73–1·20 mm
Tip of tail		With minute spur	Without spur
Females			
Length	2·25–3·82 mm	1·13–1·98 mm	4·2–5·2 mm
Maximum breadth	0·05 mm	0·06 mm	0·08 mm
Oesophagus	0·78–0·97 mm	0·38–0·49 mm	0·9–1·2 mm
Anterior end to vulva	*c.* 1·98 mm	*c.* 1·02 mm	*c.* 2·8 mm
Sperms in receptacula	—	+	+
Stage of cleavage of ova when laid	1 or 2 cell	Morula	Morula
Free-living generation			
Males			
Length	0·75–0·98 mm	0·67–0·85 mm	0·64–0·78 mm
Maximum breadth	0·04 mm	0·04 mm	0·36 mm
Tip of tail	Stiff	Flexible	Flexible
Females			
Length	0·9–1·2 mm	0·8–1·0 mm	0·73–0·86 mm
Maximum breadth	0·08 mm	0·06 mm	0·55 mm
Tip of tail	Stiff	Flexible	Flexible
Filariform larvae			
Mean length	0·50 mm	0·59 mm	0·57 mm

but did not find parasitic males. Chandler (1942), working with *S. robustus* in tree squirrels, and Melvin and Chandler (1950) working with *S. sigmodontis* in the cotton rat, failed to find parasitic males. Recsal (1951) observed the development of *S. agouti* in the guinea pig without finding parasitic males, and Rogers (1939) studied a parasite of Malayan wild cats, maintained in domestic cats, with similar results. Graham (1935 to 1940) built up an imposing body of evidence that males were not necessary at any stage in *S. ratti*. He set up infections in laboratory rats with single infective larvae derived from a homogonic strain. In this way he succeeded in

rearing 69 generations, each consisting of one female derived from a single infective larva developed directly without the intervention of a free-living sexual generation.

On the other hand, Kreis (1932) and Faust (1933) have reported finding a few parasitic males in the human parasite *S. stercoralis*. However, these organisms closely resembled the free-living males, and it seems probable that they were indeed free-living males. In Kreis' material, they developed in a culture derived from a supposedly homogonic strain; while those studied by Faust were found in the lungs of dogs infected with the human parasite. It seems possible that this development occurred because the parasite is not really well adapted to go through its normal cycle in a strange host. At all events, no one has ever found parasitic males comparable in conformation with the females in the mucosa of the small intestine.

Conclusions about the absence of males are strengthened by failure to find sperms in the female genital tract. This examination is most readily made on living material, as it is often difficult to be sure whether they are present or not in fixed material. Even finding sperms may not be conclusive evidence of the presence of males, because Sandground (1926) detected bodies, which he interpreted as sperms in the receptacula of *S. ratti*, and concluded that the worms were protandrous hermaphrodites. However, this has not been confirmed, and Chitwood and Graham (1940) considered *S. ratti* to be parthenogenetic, because they could not find sperms, nor demonstrate a vitelline membrane on the egg.

There is little stimulus to animals to differentiate, when they live in similar environments, and have similar life histories, even when the populations have been isolated from one another for long periods of time. The small morphological differences between related nematodes is therefore not surprising. *Parastrongyloides* doubtless represents the ancestral stock from which *Strongyloides* arose, and its occurrence in Australian marsupials and Palaearctic insectivores would indicate an ancient origin and considerable degree of stability. The facts presented here thus tend to support Morgan's action in erecting the genus.

References

Basir, M. A. (1950).—The morphology and development of the sheep nematode, *Strongyloides papillosus* (Wedl., 1856). *Canad. J. Res.* D **28**: 173–96.

Chandler, A. C. (1942).—Helminths of tree squirrels in south east Texas. *J. Parasit.* **28**: 135–40.

Chitwood, B. G., and Graham, G. L. (1940).—Absence of vitelline membranes on developing eggs in parasitic females of *Strongyloides ratti*. *J. Parasit.* **26**: 183–90.

Faust, E. C. (1933).—Experimental studies on human and primate species of *Strongyloides*. II. The development of *Strongyloides* in the experimental host. *Amer. J. Hyg.* **18**: 114–32.

Graham, G. L. (1935).—Single larva infections of *Strongyloides ratti* Sandground, 1925, as an approach to certain problems of *Strongyloides* bionomics. *J. Parasit.* **21**: 421–47.

Graham, G. L. (1936).—Studies on *Strongyloides*. I. *S. ratti* in parasitic series, each generation in the rat established with a single homogonic larva. *Amer. J. Hyg.* **24**: 71–87.

Graham, G. L. (1940).—Studies on *Strongyloides*. VIII. Comparison of the pure related lines of the nematode, *Strongyloides ratti*, including lines in which gigantism occurred. *J. Exp. Zool.* **84**: 241–60.

Kreis, H. (1932).—Studies on the genus *Strongyloides* (Nematodes). *Amer. J. Hyg.* **16**: 450–91.

Melvin, D. M., and Chandler, A. C. (1950).—New helminth records from the cotton rat, *Sigmodon hispidus*, including a new species, *Strongyloides sigmodontis*. *J. Parasit.* **36**: 505–10.

Morgan, D. O. (1928).—*Parastrongyloides winchesi*, gen. et sp. nov., a remarkable new nematode parasite of the mole and shrew. *J. Helminth.* **6**: 79–86.

Reesal, M. R. (1951).—Observations on the development of *Strongyloides agouti* in the guinea-pig. *Canad. J. Zool.* **29**: 116–20.

Rogers, W. P. (1939).—A new species of *Strongyloides* from the cat. *J. Helminth.* **17**: 229–38.

Sandground, J. H. (1926).—Biological studies on the life-cycle in the genus *Strongyloides* Grassi, 1879. *Amer. J. Hyg.* **6**: 337–88.

Winter, H. (1958).—Gastric strongyloidosis in kangaroos. *Aust. Vet. J.* **34**: 118–20.

THE HAEMATOZOA OF AUSTRALIAN MAMMALS

By M. Josephine Mackerras*

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Contents

Summary

Seven species of trypanosomes are known, of which *Trypanosoma binneyi* from *Ornithorhynchus anatinus*, *T. thylacis* from *Thylacis obesulus*, and *T. hipposideri* from *Hipposideros bicolor albanensis* are new. These are the first trypanosomes to be described from a monotreme, a marsupial, and an insectivorous bat in Australia.

Six species of haemogregarines are known, of which *Hepatozoon dasyuroides* from *Dasyuroides byrnei* and *H. pseudocheiri* from *Pseudocheirus laniginosus* are new.

One species of *Hepatocystis* is known from flying foxes, and one species of *Polychromophilus* from insectivorous bats.

Four species of *Babesia* are known, of which *B. thylacis* from *Thylacis obesulus* is new.

Four species of *Theileria* are known, of which *Th. ornithorhynchi* from *Ornithorhynchus anatinus* and *Th. peramelis* from bandicoots are new.

The ox is the only domestic mammal harbouring sporozoan blood protozoa, three species being known, of which two are certainly pathogenic.

Blood parasites, which appear to be related to bacteria or viruses, occur in cattle, rodents, and bandicoots. These include species of *Anaplasma*, *Haemobartonella*, and *Eperythrozoon*.

Spirochaetes belonging to the genus *Borrelia* occur in the blood of cattle, rodents, kangaroos, and bandicoots.

*Queensland Institute of Medical Research, Brisbane.

I. Introduction

Published accounts of the blood parasites of Australian animals are scattered through many journals and reports. In order to facilitate the work of subsequent observers, it is proposed to bring all the descriptions together, and to add some new ones, illustrating each species as far as possible by photomicrographs.

The first record of a blood parasite in mammals in Australia was made by T. L. Bancroft. While examining the blood of various animals for microfilariae, he noted the presence of "*Haematomonas*" (*Trypanosoma lewisi*) in the blood of rats in Brisbane (Bancroft 1888). This parasite was recorded again in Brisbane by Pound (1905), in Perth by Cleland (1906, 1908), and in Sydney by Johnston (1909).

Pound (1895) and Hunt and Collins (1896) recognized the organisms causing redwater fever in cattle. Cleland (1906) recorded *Hepatozoon muris* in rats in Perth only a few months after its discovery by Balfour in the Sudan (Balfour 1905). In December, 1907, O'Brien found malarial parasites in a flying fox at Cardwell, Qld. (O'Brien 1909). This organism was independently discovered by Breinl at Townsville in 1911, and named by him *Plasmodium pteropi* (Breinl 1913).

In Sydney, Welsh and his colleagues examined the blood of native animals whenever the opportunity occurred. They found a haemogregarine in a "flying squirrel" in 1907, and in 1909 published descriptions of it and of two other new haemogregarines in marsupials. These were the first blood parasites of mammals to be described as new in Australia.

Domestic animals are fortunately free from pathogenic trypanosomes. An outbreak of surra did occur in imported camels in 1907 in Western Australia, but Cleland sorted out the infected animals, which were then destroyed, and the disease was eradicated (Cleland 1909). Turner and Murnane (1930) showed that non-pathogenic trypanosomes occurred in sheep and cattle. We have not been so fortunate with other blood parasites of cattle, as babesiosis and anaplasmosis were introduced into the Northern Territory with the cattle tick about 1872, and spread as the tick became disseminated over a wide belt of cattle-raising country from the Kimberleys to northern New South Wales.

In this work, most attention has been paid to protozoan parasites, but other organisms which may be found in blood films are briefly mentioned. The term "Haematozoa" used in the title was chosen in order to cover all blood-dwelling organisms except microfilariae.

II. Methods

Thin blood films were dried in the air and stained with Leishman's stain, or fixed in pure methanol and stained with dilute Giemsa's stain, 1 drop per ml of distilled water buffered to pH 7·4. Prolonged staining with Giemsa (2 hr or more) was useful in bringing up the nucleus and flagellum of trypanosomes, and for rendering *Theileria* visible. Thick films were made from many animals and stained by Field's method. Sections and impression smears of organs were obtained when possible.

No one method was found to suit all parasites. Some were easily overstained with Giemsa, for example *Hepatozoon* spp. and the "malarial" parasites of Chiroptera. Others, such as *Theileria*, were invisible unless staining was prolonged.

It is well known that trypanosomes belonging to one species may vary considerably in size and shape, according to the stage of infection reached when the blood films were made. Ideally, they should be studied throughout an infection, also in culture, and inoculation into clean animals performed in order to determine the range of hosts. However, these procedures are usually extremely difficult, almost impossible tasks in practice, and, as a rule, one can only record the fragmentary information obtained from single blood films.

The classification of the protozoan parasites has been taken mainly from Kudo (1946). The terminology used by Wenyon (1926) has been adopted in the descriptions of trypanosomes. The term kinetoplast is used for the darkly staining body found near the posterior end. This body is formed of two elements, the parabasal body and the blepharoplast, from which the axoneme originates, runs along the free edge of the undulating membrane, and usually continues anteriorly as the free flagellum.

In order to save repetition, the following abbreviations have been used in giving the dimensions of trypanosomes:

L Length of body, measured along mid-line.

B Maximum breadth (including the undulating membrane), usually measured at the level of the nucleus.

PK Distance between posterior end and kinetoplast.

KN Distance between kinetoplast and posterior edge of nucleus.

NA Distance between anterior edge of nucleus and anterior end of body.

FF Free flagellum.

III. Host–Parasite List

Classification and Name of Host	Parasite
MONOTREMATA	
Ornithorhynchidae	
Ornithorhychus anatinus (Shaw, 1799), platypus	*Trypanosoma binneyi*, sp. nov. *Theileria ornithorhynchi*, sp. nov.
Tachyglossidae	
Tachyglossus aculeatus (Shaw, 1792), echidna	*Theileria tachyglossi* Priestley *Babesia* sp.
MARSUPIALIA	
Dasyuridae	
Dasyuroides byrnei Spencer, 1896, crested-tailed marsupial rat	*Hepatozoon dasyuroides*, sp. nov.
Dasyurus quoll (Zimmermann, 1777), native cat	*Hepatozoon dasyuri* (Welsh, Dalyell, & Burfitt)
Peramelidae	
Thylacis obesulus (Shaw, 1797), short-nosed bandicoot. (Queensland records = *macrourus* (Gould), which is regarded as a synonym of *obesulus*.)	*Trypanosoma thylacis*, sp. nov. *Hepatozoon peramelis* (Welsh & Dalyell) *Babesia thylacis*, sp. nov. *Theileria peramelis*, sp. nov. *Haemobartonella* sp. *Borrelia* sp.
Perameles nasuta Geoffroy, 1804, long-nosed bandicoot	*Hepatozoon peramelis* (Welsh & Dalyell) *Theileria peramelis*, sp. nov.

Classification and Name of Host	Parasite
Phalangeridae	
Petaurus breviceps Waterhouse, 1839, sugar-glider	*Hepatozoon petauri* (Welsh & Barling)
P. norfolcensis Kerr, 1792, squirrel-glider	*Hepatozoon petauri* (Welsh & Barling)
Pseudocheirus laniginosus (Gould, 1858), ring-tail possum	*Hepatozoon pseudocheiri*, sp. nov.
Macropodidae	
Potorous tridactylus (Kerr, 1792), rat-kangaroo	*Theileria peramelis*, sp. nov.
Macropus major Shaw, 1800, great grey kangaroo	*Borrelia* sp.
Macropus rufus (Desmarest, 1822), red kangaroo	*Borrelia* sp.
RODENTIA	
Muridae	
Hydromys chrysogaster Geoffroy, 1804, water-rat	*Trypanosoma lewisi* (Kent) *Haemobartonella muris* (Mayer)
Rattus assimilis (Gould, 1858), allied rat	*Trypanosoma lewisi* (Kent) *Hepatozoon muris* (Balfour) *Haemobartonella muris* (Mayer)
R. conatus Thomas, 1923, dusky field-rat	*Hepatozoon muris* (Balfour)
R. villosissimus (Waite, 1897), long-haired rat	*Haemobartonella muris* (Mayer) *Borrelia* sp.
R. norvegicus (Berkenhout, 1769), brown rat	*Trypansoma lewisi* (Kent) *Hepatozoon muris* (Balfour) *Haemobartonella muris* (Mayer)
R. rattus (Linnaeus, 1758), black rat	*Trypanosoma lewisi* (Kent) *Hepatozoon muris* (Balfour) *Haemobartonella muris* (Mayer)
Mus musculus Linnaeus, 1758, house mouse	*Eperythrozoon coccoides* Schilling
Melomys littoralis (Lönnberg, 1916), little tree-rat	*Haemobartonella muris* (Mayer)
CHIROPTERA	
Pteropodidae	
Pteropus conspicillatus Gould, 1850, spectacled flying fox	*Hepatocystis pteropi* (Breinl)
P. gouldii Peters, 1867, black flying fox	*Trypanosoma pteropi* Breinl *Hepatocystis pteropi* (Breinl)
P. poliocephalus Temminck, 1825, grey-headed flying fox	*Hepatocystis pteropi* (Breinl)
P. scapulatus Peters, 1862, little reddish flying fox	*Hepatocystis pteropi* (Breinl)
Hipposideridae	
Hipposideros bicolor albanensis Gray, 1866, dusky horseshoe-bat	*Trypanosoma hipposideri*, sp. nov.
H. semoni Matschie, 1903, horseshoe-bat	*Polychromophilus melanipherus* Dionisi

Classification and Name of Host	Parasite
Vespertilionidae	
Nyctophilus bifax Thomas, 1915, long-eared bat	*Polychromophilus melanipherus* Dionisi
Vespadelus pumilis (Gray, 1841), little bat	*Polychromophilus melanipherus* Dionisi
Miniopterus blepotis (Temminck, 1840), bent-winged bat	*Polychromophilus melanipherus* Dionisi
ARTIODACTYLA	
Bovidae	
Bos taurus Linnaeus, 1758, ox	*Trypanosoma theileri* Laveran *Babesia bigemina* (Smith & Kilborne) *Babesia argentina* (Lignières) *Theileria mutans* (Theiler) *Anaplasma centrale* Theiler *Anaplasma marginale* Theiler *Haemobartonella bovis* (Donatien & Lestoquard) *Eperythrozoon wenyoni* Adler & Ellenbogen *Borrelia theileri* (Laveran)
Ovis aries Linnaeus, 1758, sheep	*Trypanosoma melophagium* (Flu)

IV. Class MASTIGOPHORA

Genus TRYPANOSOMA Gruby

Trypanosoma binneyi, sp. nov.

Host.—*Ornithorhynchus anatinus* (Shaw).

Distribution.—Interlaken, Tas.

Type.—Slide from *O. anatinus* from Interlaken in the Queensland Museum, Brisbane.

One infected platypus was found in June, 1950, by Dr. C. A. Duncan, who exhibited the parasite at a meeting of the Royal Society of Tasmania, in Hobart, and to whom I am indebted for the type slide. Dr. Duncan suggested the specific name *binneyi* in honour of the then Governor of Tasmania, Admiral Sir Thomas Hugh Binney. The description and illustrations given below are intended to validate this name.

Morphology (*Plate* 1, *Figs.* 1–3)

The parasite is a large, broad organism, resembling the trypanosomes of some aquatic reptiles, e.g. *T. primeti* Mathis & Leger, 1909, from the water-snake (*Tropidonotus piscator*) and *T. grayi* Novy, 1906, from the crocodile (Wenyon 1926, Vol. 1, p. 584).

Cytoplasm usually heavily stained, obscuring internal structure, myonemes and scanty reddish granules present in some specimens (Fig. 3). When it could be seen, the nucleus lay near the mid-point of the body, close to the origin of the undulating membrane (Fig. 3). Kinetoplast small, rounded, or rod-like. Undulating membrane well developed, with numerous undulations (Fig. 1), free flagellum short and palely stained (Fig. 2). Anterior end long, narrow, and palely stained.

Dimensions.—L, 47–67 μ; B, 11–15 μ; PK, 11–18 μ; KN, *c.* 14 μ; NA, 17–37 μ; FF, 7–12 μ.

Discussion

Fleas have not been reported on the platypus, but it has a tick, *Ixodes ornithorhynchi* Lucas, which is peculiar to it. The animals are also liable to be bitten by blood-sucking flies and leeches, so that the number of possible intermediate hosts is large.

Recently Mr. J. H. Calaby, Wildlife Survey Section, C.S.I.R.O., Canberra, drew my attention to an earlier record of trypanosomes in a platypus. Dr. W. J. Owen, Australian Institute of Anatomy, Canberra, recorded their presence in a communication read before the Royal Society of Australia in Canberra on September 25, 1933. A year later he demonstrated their presence in the blood vessels of the adrenal gland of another platypus. Owen gave the average length of the trypanosomes as 75 μ, and published a photomicrograph of one, but did not suggest a specific name. The illustration shows a very long, rather slender trypanosome, with a particularly attenuated posterior end, and a narrow undulating membrane. This organism does not look very like any of those seen in the film from the Tasmanian platypus, and may possibly be distinct.

Trypanosoma thylacis, sp. nov.

Trypanosoma sp., Mackerras, Mackerras, and Sandars, 1953, p. 61.

Host.—*Thylacis obesulus* (Shaw).

Distribution.—Brisbane.

Type.—Slide from *T. obesulus* from Brisbane in the Queensland Museum, Brisbane.

Infections were found in 12 out of 82 bandicoots examined from the suburbs of Brisbane. Nearly all the infected animals came from one or other of two suburbs. Trypanosomes were never easy to find, even in thick films, and it is probable that many light infections were missed. An infected animal was kept in the laboratory for 7 weeks, during which time its blood was examined on 25 occasions. Trypanosomes were present at each examination, but always in low density. Blood films were also examined from numerous bandicoots from Innisfail, N. Qld. No trypanosomes were seen in them, but crithidial forms and trypanosomes grew on one occasion in a culture of kidney which was made in a survey for leptospirae.

Morphology (*Plate* 1, *Figs.* 4–6)

This is a graceful species of moderate size. The forms seen in the blood were rather uniform in appearance, being moderately broad, with well-developed flagellum and undulating membrane, the latter with a few large undulations. The cytoplasm was usually clear or occasionally granular. The kinetoplast was oval or rod-shaped, situated a considerable distance from the posterior end. The nucleus was rounded, granular, or reticular, about 2 μ in diameter, and usually central in position. In wet preparations they progressed with moderate speed, either forward or backward, with

rapid movement of the undulating membrane and flagellum. The long, finely tapered, posterior end appeared stiff in life.

Dimensions of forms in the peripheral blood.—L, 22–32 μ; B, 5–7·5 μ; PK, 6–11 μ; KN, 4–6 μ; NA, 10–16 μ; FF, 8–12 μ.

Flagellates in Tissues other than Blood

Trypanosomes were found accidentally in the tissue fluids of four bandicoots. During an investigation of bandicoot filariae, smears were made from broken female worms (*Dipetalonema johnstoni* Mackerras) dissected from the subcutaneous tissue, in order to study the appearance of microfilariae liberated from the uterus of the parent worm. On two occasions, a few small, fast-moving, flagellate organisms were seen in these preparations. On another occasion, similar flagellates were in the serous fluid expressed from a skin snipping, which was being examined for microfilariae, and in the fourth animal they were seen in company with microfilariae in lymph from an axillary lymph gland.

In stained films these proved to be very slender trypanosomes. The undulating membrane was poorly developed, and the body so narrow that it was difficult to define the anterior tip; the free flagellum was fairly long. The kinetoplast was usually just posterior to the nucleus (Plate 1, Fig. 7).

Dimensions of forms from tissue.—L, 19–22 μ; B, 1–1·7 μ; PK, 6–7 μ; KN, 1·8–2·5 μ; NA, 8–11 μ; FF, 10·5–14 μ.

The significance of the slender trypanosomes is not known. Their association with filarial infection is remarkable. Normal blood-dwelling trypanosomes were not detected in a long search of the blood films from the four animals in question, but they may have been present in small numbers.

On one occasion, a single slender trypanosome was seen in a wet preparation of peripheral blood of another bandicoot, but no flagellates at all were found in the stained films. This is the only occasion on which a slender trypanosome was seen in an animal not harbouring filariae, but it came from a locality where filariated bandicoots had been obtained.

Experimental

(i) Attempts to transmit *T. thylacis* to laboratory animals were unsuccessful. Citrated heart blood from an infected bandicoot was injected intraperitoneally into very young guinea pigs, rats, and mice, but no trypanosomes were ever detected in the blood films of inoculated animals. Known clean bandicoots were not available at this time.

(ii) Later, a scanty infection was found in a captured bandicoot, and approximately 3 ml of citrated heart blood from this animal was injected intraperitoneally into each of three bandicoots, which had been reared in the laboratory from the pouch young state from 15 months to 2 years and 5 months previously. No trypanosomes were found in blood films from these animals, except a single organism in one animal on the 5th day, and a single organism in another animal on the 21st day. They appeared to be unchanged in size and conformation.

(iii) Flagellates were grown once on N.N.N. medium from a fragment of the spleen of a bandicoot, in which a single trypanosome similar to the blood form had been found in a stained film. The flagellates varied considerably in size and shape. Small, rounded, *Leishmania*-like forms, crithidial forms, and trypanosomes were present (Plate 1, Figs. 8–10). Some trypanosomes were thinner than that shown in Plate 1, Figure 10, almost as attenuated as those in tissue fluids (Plate 1, Fig. 7), or as those from ticks described below (Plate 1, Fig. 11).

Dimensions of flagellates in N.N.N. Medium.—Leishmania forms: 3 by 3 μ–8 by 6 μ. Crithidial forms: 10 by 2 μ–15 by 1·5 μ; FF, 6–9 μ. Trypanosomes: L, 23–27 μ; B, 1·5–2 μ; PK, 5·5–9 μ; KN, 6·5–7·5 μ; NA, 6–7 μ; FF, 6–10 μ.

A rich suspension of flagellates from a 12-day culture was injected intraperitoneally into two young bandicoots, which had been under observation for the previous 2 months, one having been reared in the laboratory. Thick and thin blood films were examined daily for 8 days, and then thrice weekly for 10 weeks, but no trypanosomes were seen. After 3 weeks cardiac puncture was performed, and blood inoculated into N.N.N. medium. Approximately 1 ml from each animal was laked with distilled water, centrifuged, and the sediment examined, but no trypanosomes were found.

(iv) The flagellates, which were grown in the culture on Schüffner's medium from the kidney referred to above, were also rather similar to the tissue forms. However, they were slightly broader, the posterior end was definitely blunter, and the flagellum was usually much shorter. A few approached the crithidial form, but the kinetoplast of most lay just posterior to the nucleus. Some *Leishmania* forms were also seen. Although cultures for leptospirae have been made from the kidneys of over 300 bandicoots from north Queensland, flagellates were grown only on this one occasion.

Dimensions of flagellates in Schüffner's medium.—L, 17–26 μ; B, 1·8–3 μ; PK, 6–11·5 μ; KN, 1–2 μ; NA, 7·5–10 μ; FF, 3·5–8 μ.

Schüffner's medium containing numerous organisms was injected into two bandicoots and two white mice, but no trypanosomes were found in blood films made subsequently from any of the recipients.

Discussion

It has not been possible to link these various forms together, but one may suspect that they will eventually prove to be stages of one organism. In Europe, *T. vespertilionis* of bats has been observed to multiply by repeated binary fission in cysts in various organs, large numbers of small slender trypanosomes being produced (Wenyon 1926, p. 481). I have not been able to demonstrate a similar process in bandicoots, but, if it occurred, it could account for the slender tissue forms.

A possible link was suggested by finding very scanty slender trypanosomes in the gut contents of both of two nymphs of *Ixodes holocyclus* (Neumann) removed from a captured adult bandicoot (No. 506). These trypanosomes (Plate 1, Fig. 11) were similar to those found in subcutaneous tissue.

Dimensions of trypanosomes from ticks.—L, 18–20 μ; B, 1–2 μ; PK, 6–7·5 μ; KN, 1·5–2·5 μ; NA, 6·5–9·5 μ; FF, 9–11 μ.

The blood of No. 506 was examined on numerous occasions, heart blood was cultured, concentration of about 2 ml attempted, and a skin snipping was examined but no trypanosomes were found.

Trypanosoma lewisi (Kent)

Herpetomonas lewisi Kent, 1880–1, p. 245.

Hosts.—*Rattus rattus* (L.), *R. norvegicus* (Berkenhout), *R. assimilis* (Gould), *Hydromys chrysogaster* Geoffroy.

Distribution.—Probably cosmopolitan. Recorded from Queensland, New South Wales, and Western Australia.

This species has been recorded on several occasions in Australia, by Bancroft (1888) and Pound (1905) in Brisbane, by Cleland (1906, 1908) in Perth, by Johnston (1909) in Sydney, and by Breinl (1913), who found it in about 15 per cent. of rats in Townsville.

Morphology (*Plate* 2, *Figs.* 1 *and* 2)

When young rats are inoculated with blood containing *T. lewisi*, there ensues a period when the parasites multiply rapidly, followed by a chronic phase, when multiplication ceases, the parasites gradually diminish in numbers, and finally disappear from the circulation.

During the phase of multiplication (Fig. 1) the parasites vary greatly in size and dividing and crithidial forms may be found in the peripheral blood. The nucleus is rounded and usually anterior to the mid-point. The posterior end is long and sharply pointed and the undulating membrane is not well developed, except in the largest forms. This phase merges gradually into the chronic phase, in which all the organisms are slender trypanosomes of fairly uniform size (Fig. 2). The posterior end is sharply pointed and the kinetoplast is nearer to it than in the earlier phase. The nucleus is oblong and definitely in the anterior half of the body. The undulating membrane is poorly developed. The measurements for the chronic phase given below were taken from a natural infection in a wild brown rat.

Dimensions.—Phase of multiplication: L, 11–30 μ; B, 1·5–5 μ; PK, 3–9 μ; KN, 2–11 μ; NA, 2–9 μ; FF, 7–10 μ. Chronic phase: L, 23–27 μ; B, 2–2·5 μ; PK, 2–3·5 μ; KN, 9–11 μ; NA, 6–10 μ; FF, 6–11 μ.

This species has been quite frequently seen in both species of introduced rats taken at Brisbane, and in *R. rattus* at Innisfail, N. Qld., particularly in young animals. Trypanosomes, which appear to be identical, have been found in 3 out of 9 *R. assimilis* from Mt. Glorious, S. Qld., and in 3 out of 38 of the same species from Innisfail. The parasites were transmitted to laboratory rats from one of the Mt. Glorious specimens. Similar trypanosomes were seen in 1 out of 37 *H. chrysogaster* from Innisfail.

Life History

In Europe, the parasite has been found to be transmitted by the rat flea, *Nosophyllus fasciatus* (Bose d'Antic), and experimentally by many other species.

The trypanosomes go through a cycle of development, culminating in the production of metacyclic forms in the rectum of the flea. Infection of the rat occurs when it eats an infected flea or its faeces. Transmission by biting does not occur.

Trypanosoma pteropi Breinl

Trypanosoma pteropi Breinl, 1913, p. 30.

Host.—*Pteropus gouldii* Peters.

Distribution.—Townsville, Cairns, N. Qld.

Breinl found only a scanty infection in 1 out of about 25 flying foxes examined. His description may not be readily available, so it is given here.

"The trypanosome possesses a slender body, and has a pointed blepharoplastic end. The blepharoplast is large, and seems to consist of two ring-shaped chromatin masses, which are placed in the shape of a cross. In nearly all specimens a vacuole was present in front of the blepharoplast; the nucleus does not show any characteristic features. The parasite has a long, free flagellum; the undulating membrane is not well developed.

The few trypanosomes found were of approximately the same size; the distance from the blepharoplastic end to the blepharoplast measured 2·5 to 3 μ. The nucleus was 5·6 to 7 μ distant from the blepharoplast. The total length averaged between 20 to 22 μ. The width at the level of the nucleus was 2·5 to 3 μ; the free flagellum averaged 11–12 μ."

Small trypanosomes were found in the blood of a flying fox (*Pteropus* sp.) from Cairns (Plate 2, Figs. 3–5). They agreed closely with Breinl's description, except that they were slightly smaller, and the kinetoplast was usually round. The anterior end was sharply pointed. One broad form was seen, 7·5 μ in diameter; its other dimensions were not increased, its cytoplasm appeared very thin, and, as other burst forms were seen in the vicinity, it was thought that it was probably about to disintegrate. It was not included in the measurements given below, which were taken from nine consecutive trypanosomes found.

Dimensions.—L, 18–20 μ; B, 2–4 μ; PK, 1·5–4 μ; KN, 4–5 μ; NA, 8–10 μ; FF, 8–10 μ.

This species seems to be close to *T. vespertilionis* Battaglia, 1904, which has been found frequently in European bats belonging to the family Vespertilionidae. *T. vespertilionis* is said to resemble *T. cruzi*, and it is noteworthy that both these species reproduce in organs.

Trypanosoma hipposideri, sp. nov.

Host.—*Hipposideros bicolor albanensis* Gray.

Distribution.—Innisfail, N. Qld.

Type.—Slide from *H. bicolor albanensis* from Innisfail in the Queensland Museum, Brisbane.

A scanty infection was found in blood films from a dusky horseshoe bat, forwarded by Miss M. L. Emanuel from the Institute's Field Station at Innisfail.

Morphology (*Plate* 2, *Figs.* 6–8)

A very small slender species, the posterior end pointed in some, rounded in others; kinetoplast relatively large, situated near posterior end; nucleus usually oval,

situated in the anterior half of the body; free flagellum short and delicate. The parasites were fairly uniform in size and no dividing forms were seen.

Dimensions.—L, 10·5–13 μ; B, 1·5–2 μ; PK, 1–2·5 μ; KN, 4–6 μ; NA, 1·5–5 μ; FF, 4–8 μ.

This species differs considerably from two trypanosomes described from bats belonging to the genus *Hipposideros*, namely, *T. morinorum* Leger & Baury from *H. tridens* of Senegal, and *T. leleupi* Rodhain from *H. caffer* of the Belgian Congo. *T. morinorum* is a relatively large organism, 30 by 7–8 μ, with the kinetoplast situated near the centrally placed nucleus. *T. leleupi* is even longer, and quite distinctively shaped, with attenuated ends and broad middle section; the body is 32 by 6 μ, the free flagellum 12 μ; the kinetoplast is situated a long way from the sharply pointed posterior end, and separated from the nucleus by a distance of about half the body width (Leger and Baury 1923; Rodhain 1951).

T. hipposideri is smaller than *T. vespertilionis* and *T. pteropi*, the free flagellum is shorter and more delicate, and the nucleus closer to the anterior end.

Trypanosoma theileri Laveran

Trypanosoma theileri Laveran, 1902, p. 512.

Host.—Bos taurus L.

Distribution.—Probably cosmopolitan, wherever cattle occur.

This species is non-pathogenic. Turner and Murnane (1930) found trypanosomes in 1 out of 12 specimens of bovine blood collected at the abattoirs in Melbourne. Large amounts of blood were laked, centrifuged, and the sediment examined.

Morphology (*Plate* 2, *Fig.* 9)

This is a large trypanosome, frequently showing well-marked myonemes. There is considerable variation in the position of the kinetoplast. Wenyon (1926) records large forms 60–70 μ long by 4–5 μ wide. and also smaller forms 25–30 μ long. Turner and Murnane gave measurements intermediate between these two forms. Two specimens gave the following measurements in microns:

Dimensions.—L, 47·5, 56·0; B, 3·75, 4·0; PK, 9·0, 11·0; KN, 9·0, 8·0; NA, 25·0, 28·5; FF, 5·0, 10·0; nucleus, 4·5 by 1·75, 5·0 by 2·5.

Life History

Tabanid flies are considered to be the vectors. In Europe, *Haematopota pluvialis* (L.) has been shown to carry the infection, crithidial forms obtained in culture from a fly setting up infection (proved by culture) in clean calves when injected into them (Nöller 1925). Hoare (1949) stated that development in the fly is in the posterior station, and that infection is by contamination.

Trypanosoma melophagium (Flu)

Crithidia melophagia Flu, 1908, p. 153.

Host.—Ovis aries L.

Distribution.—Probably cosmopolitan, wherever sheep occur.

This is also a non-pathogenic species. Turner and Murnane (1930) found infections in 8 out of 10 sheep by the use of concentration methods. They set up a heavy infection in a clean, splenectomized lamb by feeding it numerous keds from other sheep. The species is apparently quite common, for crithidial forms were found readily in keds at Canberra, although trypanosomes were not seen in the sheep.

Morphology (*Plate* 2, *Fig.* 10)

T. melophagium is a large organism, with both ends of the body sharply drawn out. The undulating membrane is not particularly well developed, showing only a few undulations. The free flagellum is short. Turner and Murnane gave the following measurements of forms seen by them.

Dimensions.—L, 30–50 μ; B, 2–3 μ; PK, 10–17 μ; KN, 4–9 μ; NA, 19–22 μ; FF, 2·5–6 μ.

Life History

The stages in the ked, *Melophagus ovinus* (L.), were studied before those in the blood of sheep, the organism being described as *Crithidia melophagia*, and considered to be peculiar to the insect. Metacyclic trypanosomes are produced in the hindgut, and infection takes place by ingestion. The bite of an infected ked does not cause infection.

V. Class SPOROZOA

The sporozoan blood parasites of mammals belong to two orders, the Coccidia, represented only by the genus *Hepatozoon*, and the Haemosporidia, which is an assemblage of convenience containing three families and a moderate number of genera. Most are characterized by well-marked anisogamy; so, if Dennis' (1931) observation that *Babesia* produces isogametes is confirmed, and extended to other members of the family, it may prove necessary to transfer the Babesiidae to the suborder Adeleidea of the Coccidia, near *Hepatozoon*.

In the Haemosporidia, as at present recognized, no representatives of the genus *Plasmodium* have been found yet in native mammals, although they occur in birds and reptiles. The pigmented parasites found in the Australian Chiroptera appear to be more closely allied to *Haemoproteus* than to *Plasmodium*, and have been placed in two genera, *Hepatocystis* and *Polychromophilus*, of the family Haemoproteidae.

In other parts of the world four genera are known from Chiroptera: (i) a true *Plasmodium*, (ii) *Hepatocystis*, (iii) *Polychromophilus*, and (iv) *Nycteria*. Schizonts are found in red cells in *Plasmodium*, but in the other genera only gametocytes occur in red cells. Large exo-erythrocytic schizonts occur in the liver in all except *Polychromophilus*. *Hepatocystis* is characterized by large, irregular, cystic schizonts in the liver; *Nycteria* by large solid schizonts in the same organ, superficially resembling those of *Plasmodium falciparum* in man, but differing in nuclear structure; *Polychromophilus* by minute schizonts in reticulo-endothelial cells.

Non-pigmented parasites belonging to the Babesiidae occur in monotremes and marsupials, and introduced species in cattle. These important parasites of stock will only be mentioned briefly here, as they are fully dealt with in textbooks of veterinary parasitology.

Genus HEPATOZOON Miller

Wenyon (1926) placed all the haemogregarines of mammals in the genus *Hepatozoon*. These parasites fall into two groups, one in which the gametocytes are found in leucocytes, and the other in which they occur in red cells. A good deal of information is available in the literature about the first group, members of which have been shown to be carried by mites or ticks. The formation of large oocysts in the coelom of the intermediate host is a characteristic feature. Infection of the vertebrate host is by ingestion.

Much less information seems to be available about the second group. Christophers (1905) described *H. gerbilli* of the gerbil, and consistently found large oocysts in the coelom of lice, *Haematopinus stephensi*, taken from infected gerbils. He examined the tissues of two heavily infected gerbils, but did not find schizonts. The organs searched included spleen, liver, bone marrow, kidneys, lungs, testes, thymus, thyroid, suprarenals, brain, muscles, and lymphatic glands. Scrapings were also made from many levels in the alimentary tract, but no developmental stages were detected. Balfour (1906), on the other hand, found schizonts in the livers of jerboas, *Jaculus gordoni*, infected with *H. balfouri* Laveran, but the invertebrate host was not found.

Characteristic oocysts have been recorded in a sandfly (*Phlebotomus*), but these have not been linked with any particular species of *Hepatozoon*. Hoare (1932) showed that the haemogregarine of the crocodile, *Hepatozoon pettiti* (Thiroux) develops in a tsetse fly, *Glossina palpalis*, very large oocysts being found in its coelom. It is, therefore, evident that a wide range of arthropods may be involved as intermediate hosts.

In Australia, *H. muris* of introduced and native rats is the only common member of the group infecting leucocytes. *Hepatozoon* sp. (presumably *canis*) was seen once in liver sections of a dog (Bull 1914). The parasites of marsupials belong to the second group, all of the five known species inhabiting red cells. They vary considerably in size, three being long, thin organisms, and two being relatively short. Some at least are clearly enclosed in a capsule. Some resemble *H. gerbilli* very closely.

Similar parasites occur in the red cells of American opossums: *H. didelphydis* (d'Utra, Silva, & Arantes, 1917) in *Didelphys aurita* in Brazil, and an unnamed species in *Metachirops opossum* from British Honduras (Garnham and Lewis 1958). Schizonts were found in the pancreas of *D. aurita*.

Hepatozoon muris (Balfour)

Leucocytozoon muris, Balfour, 1906, p. 111.
Hepatozoon muris (Balfour, 1906), Wenyon, 1926, p. 1086.

Hosts.—*Rattus rattus* (L.), *R. norvegicus* (Berkenhout), *R. assimilis* (Gould), and *R. conatus* Thomas.

Distribution.—Probably cosmopolitan. Known from Western Australia, New South Wales, and Queensland.

It was recorded in Australia by Cleland (1906, 1908) in Perth, and by Johnston (1909) in Sydney.

Morphology (*Plate* 3, *Figs.* 1–3)

The gametocytes are short, oval, encapsulated parasites, 7–8 μ by 3–3·5 μ, with a central nucleus, occurring in the monocytes. The nucleus of an infected cell becomes indented, and sometimes separated into two parts (Fig. 2). All the forms in the peripheral blood are similar in size and shape.

Schizonts are found in the liver, where they form conspicuous round or oval bodies up to 30 μ in diameter, containing numerous elongate merozoites (Fig. 3). These merozoites may infect other liver cells, but after a few cycles they invade the mononuclear leucocytes, and grow into gametocytes, which only develop further when taken up by the intermediate host.

Typical gametocytes have been found in the monocytes of two species of wild rats. They were present in 3 out of 9 *R. assimilis* from Mt. Glorious, S. Qld., in 13 out of 38 of the same species from Innisfail, N. Qld., and in 1 out of 16 *R. conatus* from Innisfail.

Life History

The vector is the mite, *Laelaps echidninus* Berlese. Large oocysts, up to 200 μ in diameter, are formed in the coelom of the mite. Each oocyst divides into a number of sporocysts, each of which eventually contains 12–24 sporozoites. New hosts are infected by eating infected mites. The laelaptid mites are, in general, active creatures, which habitually run off and on their host, and in this way pass from rat to rat when the animals are congregated together. A laboratory rat was infected by feeding it pooled mites from wild *Rattus norvegicus* in Brisbane.

HEPATOZOON PETAURI (Welsh & Barling)

Haemogregarina petauri Welsh and Barling, 1909, p. 329; 1910, p. 536.
Hepatozoon petauri (Welsh and Barling, 1909), Wenyon, 1926, p. 1362.

Hosts.—*Petaurus norfolcensis* Kerr and *P. breviceps* Waterhouse.

Distribution.—Sydney and Glen Davis, N.S.W.; ? Brisbane.

In Sydney, in October 1907, Welsh and Barling studied an abundant infection in blood films from an adult male "flying squirrel", one of a family kept as pets. No parasites were found in the others, a female and a young one. The host was said to be *Petaurus* sp. probably *sciureus*, a name now considered to be a synonym of *norfolcensis*.

Morphology (*Plate* 3, *Figs.* 4–6)

The following is a summary of the authors' description. Elongate, oval parasites, 7·5–8 μ by 3·5–4 μ, roughly cylindrical in outline, with rounded ends. A "tail" was not observed. Cytoplasm was finely granular, with few vacuoles. The subterminal nucleus occupied about two-fifths of the total length, and showed central and peripheral condensations; its polar extremity was capped by a thin crescent of condensed cytoplasm. Scattered chromatin granules were present in the cytoplasm of some specimens. There was some variation in size, but practically none in general form. One doubly infected cell was seen, the small parasites measuring 5 by 2·5 μ. The parasites were almost all intracellular, and infected cells were slightly enlarged and paler than normal.

A scanty infection was present in films from *P. breviceps* sent to me by the Reverend R. Palmer of Glen Davis, N.S.W. The parasites agreed with the above description in having a terminal, or subterminal, nucleus, composed of a ring of chromatin with a pale centre, granular cytoplasm, and in causing slight enlargement and definite pallor of the host red cell. However, the polar cap of condensed cytoplasm and the chromatin granules described by Welsh and Barling were not seen. In nearly every infected cell there was present an indefinite wavy structure attached to the parasite and projecting into the host cytoplasm as a loop (Figs. 4–6). Its function is unknown.

Films from the same species of glider from the Botanic Gardens, Brisbane, contained parasites which were considerably larger, measuring about 10 by 6 μ, filling an enlarged red cell. The nucleus was large, central to subterminal in position, showing a granular or lattice-like structure, with thickenings along the strands of the lattice work. The cytoplasm was usually clear and scarcely stained (Plate 3, Figs. 7 and 8). This may possibly be a stage of *H. petauri*, but more probably is a distinct species. It bears some resemblance to *H. didelphydis* in the South American opossum, *Didelphys aurita*, as described by d'Utra, Silva, and Arantes (1917). It seems better to wait until the life history of *H. petauri* has been worked out before suggesting a new name for it.

Hepatozoon dasyuri (Welsh, Dalyell, & Burfitt)

Haemogregarina dasyuri Welsh, Dalyell, and Burfitt, 1909, p. 333; 1910, p. 543.
Hepatozoon dasyuri (Welsh, Dalyell, and Burfitt, 1909), Wenyon, 1926, p. 1357.

Host.—*Dasyurus quoll* (Zimmermann), previously known as *D. viverrinus* (Shaw).

Distribution.—Sydney.

Up till June, 1908, Welsh and his colleagues had examined about 50 dasyures, parasites being found in only one. It therefore appeared to be a rather uncommon parasite. Now the host has become very uncommon too, and it is unlikely that anyone will be able to examine many native cats in future.

Morphology

Three main types were distinguished: (i) completely flexed, (ii) semi-flexed, and (iii) unflexed. There was a sharply defined capsule. The completely flexed forms were larger than the average red cell. There was a large, oval nucleus showing a reticular structure. Cytoplasm homogeneous or slightly granular, containing minute red dots in anterior part. The unflexed forms measured about 12 by 4 μ; the large, centrally placed nucleus filled the body for about one-quarter of its length; the red cell was greatly stretched and decolourized. Free vermicules were occasionally seen, measuring 21 by 3 μ: one end was broader and contained chromatin dots. This was regarded as the anterior end. The life history is unknown.

Hepatozoon peramelis (Welsh & Dalyell)

Haemogregarina peramelis Welsh and Dalyell, 1909, p. 112; 1910, p. 547.
Hepatozoon peramelis (Welsh and Dalyell, 1909), Wenyon, 1926, p. 1361.

Hosts.—*Perameles nasuta* Geoffroy (type host), and *Thylacis obesulus* (Shaw).

Distribution.—Thirroul, N.S.W. (type locality); Gympie and Brisbane, S. Qld., Innisfail, N. Qld.

Morphology (*Plate* 3, *Figs.* 15–17)

Welsh and Dalyell studied a scanty infection in films from a long-nosed bandicoot. They described the parasites as extracellular, 9–10 μ by 3–3·5 μ. The nucleus lay in the narrower half of the parasite, measuring 3·5 μ, and consisting of a limiting membrane containing irregular masses of chromatin or a well-marked reticulum. Cytoplasm hyaline, occasionally stippled.

I have seen numerous infections in short-nosed bandicoots in Queensland. At Innisfail, about one-third of those examined had at least a scanty infection. In south Queensland, the infection seems to be less common. One infected animal was kept under observation for over 3 months, during which time blood films were made on 20 occasions. Fairly numerous parasites were found at each examination.

In some films, extracellular parasites were seen, but intracellular forms were always present as well. Infected cells were enlarged, oval, usually about 10 by 8 μ, and stained reddish. In some bandicoots the cells were particularly large and distorted. The parasite usually lay obliquely across the cell; the nucleus was large, reticular, and subterminal. The organism was contained in a capsule, with the narrower end flexed beneath. Occasionally two parasites were present in a cell (Fig. 17).

Sections of organs from two infected bandicoots were searched, as well as numerous sections of other bandicoots which could possibly have been in the early stages of infection, but nothing resembling the schizonts of *H. muris* were seen.

Life History

Unknown. Some ectoparasites from a bandicoot with a moderate infection were examined, but no intermediate stages were found. These included 2 nymphs of *Ixodes holocyclus* (Neum.), 16 fleas, comprising 14 *Stephanocercus dasyuri* Skuse and 2 *Pygiopsylla* sp., 4 mites, 1 *Mesolaelaps antipodianus* (Hirst), and 3 *Haemolaelaps marsupialis* Berlese. Efforts to transfer mites from non-infected bandicoots to the infected animal were unsuccessful, the ectoparasites quickly disappearing. Of 5 mosquitoes (*Culex fatigans* Wied.) which fed on the infected bandicoot, 3 survived for 3 weeks, but no developmental stages were found in them.

HEPATOZOON PSEUDOCHEIRI, sp. nov.

Host.—*Pseudocheirus laniginosus* (Gould).

Distribution.—Mt. Nebo, S. Qld.

Type.—Slide from *P. laniginosus* in the Queensland Museum, Brisbane.

I have seen a moderately numerous infection in the only ring-tailed possum examined from Mt. Nebo. The parasites were not seen in ring-tails taken near Brisbane.

Morphology (*Plate* 3, *Figs.* 9–11)

Long, relatively thin organisms, acutely flexed within a definite capsule, which measured 6·5–8 μ by 4·5–6·5 μ, the parasites themselves being 8–13 μ by 1·5–3 μ. One end was slightly broader than the other, paler in colour, and usually free from granules. The nucleus was large, oblong, situated close to the broader end. The infected red cells were slightly enlarged and definitely paler than normal cells.

This species is close to *H. dasyuri*, and may prove to be a synonym of it. The hosts have a similar distribution around the eastern and southern parts of Australia. Native cats are terrestrial and to some extent arboreal; ring-tailed possums are arboreal, although some of their relatives have taken to a terrestrial existence in the northern and western ends of their range.

The chief differences seen are in size, *H. pseudocheiri* being slightly smaller than *H. dasyuri*, and not filling the red cell, as *H. dasyuri* was shown to do. The life history is unknown.

HEPATOZOON DASYUROIDES, sp. nov.

Host.—*Dasyuroides byrnei* Spencer, 1896.

Distribution.—Birdsville, south-western Qld.

Type.—Slide from *D. byrnei* from Birdsville in the Queensland Museum, Brisbane.

Two fairly numerous and 3 scanty infections were found out of 7 males examined at the Queensland Museum.

Morphology (*Plate* 3, *Figs.* 12–14)

Long, narrow parasites, 12–13 μ by 1–2 μ, usually lying with the narrower end slightly flexed, but sometimes almost straight or only slightly curved along the margin of the greatly expanded red cell. No cytocyst was detected. Infected cells measured 11–12 μ by 8–9 μ, a normal cell being about 6 μ in diameter. The cytoplasm of the parasite usually stained pale blue, and occasionally some reddish granules were present in it. The nucleus was 3–4 μ long, filling almost the entire width of the parasite.

This species is slimmer than *H. dasyuri*, and does not appear to have a capsule; it causes more distension of the red cell.

The hosts belong to different subfamilies of the Dasyuridae. Their distributions do not overlap, *Dasyurus quoll* inhabiting the well-wooded parts of eastern and southern Australia, whereas *Dasyuroides byrnei* is confined to the arid central parts of Australia. The life history is unknown.

Genus HEPATOCYSTIS Levaditi & Schoen

HEPATOCYSTIS PTEROPI (Breinl)

Plasmodium pteropi Breinl, 1913, p. 35.
Hepatocystis pteropi (Breinl, 1913), Lawrence, 1955, p. 61.

Hosts.—*Pteropus gouldii* Peters (type host), *P. conspicillatus* Gould, *P. poliocephalus* Temminck, and *P. scapulatus* Peters.

Distribution.—Townsville, Cardwell, Innisfail, Cairns, Mossman, N. Qld.

This is a common parasite of flying foxes in north Queensland. It was first seen by O'Brien in a flying fox shot at Cardwell in December, 1907 (O'Brien 1909), and discovered independently by Breinl in Townsville in 1911. Bearup and Lawrence (1947) found 50 out of 54 adults and 12 out of 40 young (1–3 months old) to be infected. It has also been recorded in the New Hebrides, and similar, if not identical. parasites are known in Africa and India. Manwell (1946) found what may prove to be a different species in the related genus *Dobsonia* in New Guinea. Bats belonging to *Dobsonia* have not yet been examined in Australia.

Morphology (*Plate* 4, *Figs.* 1–6)

Breinl (1913) described young ring forms with a large vacuole and fine pigment and larger amoeboid forms with coarser pigment. Gametocytes were fairly common, microgametocytes had light-bluish cytoplasm and diffuse eccentric nucleus, and macrogametocytes had dense dark blue cytoplasm and dense nucleus. Both had coarse yellowish brown pigment. Breinl remarked on the absence of mature schizonts, and his figures of what he thought were possibly early schizonts may represent microgametocytes. Manwell (1946) found unpigmented schizonts in peripheral blood smears of *P. gouldii* from New Guinea.

Lawrence (1955) found merocysts, typical of the genus *Hepatocystis*, in sections of the liver of two *P. scapulatus* from Townsville. These merocysts were relatively large, 0·25 mm or more in diameter, with irregular lobulated edges composed of very numerous merozoites (Figs. 1 and 2). Possibly the schizonts seen by Manwell were portions of one of these merocysts forced into the circulation after trauma to the liver.

Typical rings and gametocytes were found in 5 out of 7 *P. conspicillatus* from Innisfail and Mossman (Figs. 3–6), and in an unrecorded number of the same species, and in *P. gouldii*, and *P. poliocephalus* from Cairns and Townsville. Sections from the liver of one of the last-named showed granulomata but no schizonts.

Life History

Unknown. Bearup and Lawrence (1947) made an extensive search for the intermediate host but without success. They dissected 334 mosquitoes, belonging to different species of *Anopheles*, *Culex*, and *Aedes*, which had fed on flying foxes with gametocytes in the blood. They also dissected 49 *Cyclopodia albertsii* Rondani, the common nycteribiid of flying foxes, as well as various species of biting flies collected near their camps, where the presence of infected young indicated that transmission was occurring. No developmental stages were found in any of these insects.

It seems unlikely that mosquitoes of the genera studied are the intermediate hosts, but we know nothing of the canopy mosquito fauna, which might be attacking the resting flying foxes, and Simuliidae have not yet been tried.

The vector of *Hepatocystis kochi* (Levaditi & Schoen) of monkeys is also unknown, in spite of an even more comprehensive search. Garnham (1951, 1957)

examined many biting arthropods and even blood-sucking nematodes. Some development took place in mosquitoes but no oocysts nor sporozoites were found. Ticks, mites, lice, reduviid bugs, and sandflies (*Culicoides*) were tried unsuccessfully. More recently Bauer and Hohorst (1958) took lice (*Pedicinus patus*) from heavily infected monkeys, ground them up, and injected them into two clean monkeys but no parasites appeared in the recipients' blood.

Genus POLYCHROMOPHILUS Dionisi

Polychromophilus melanipherus Dionisi

Polychromophilus melanipherus Dionisi, 1899.

P. melanipherus was originally described by Dionisi from the European bent-winged bat, *Miniopterus schreibersi*. The parasites seen in insectivorous bats in Queensland have been referred to this species because they appear similar in morphology, and because the Australian bat, *Miniopterus blepotis*, is now regarded by many zoologists as identical with *M. schreibersi*. At any rate, closely related, if not identical, bats range from Europe through Asia and the Malay Archipelago to Australia.

I have seen scanty infections in 3 out of 16 *Vespadelus pumilis* taken from a cave near Upper Teviot Brook, S. Qld., collected by Mr. K. Harley; in 3 out of 23 *Miniopterus blepotis* from a cave in Mt. Pleasant, S. Qld., collected by Dr. P. Morrison; in 1 out of 2 *Nyctophilus bifax* from Mossman, N. Qld., collected by Miss M. L. Emanuel; and a heavier infection in 1 *Hipposideros semoni* from the Lockhart River Mission, N. Qld.

Morphology (*Plate* 4, *Figs.* 7–10)

Only gametocytes have been found. The mature gametocyte filled the red cell, which was slightly enlarged. Microgametocytes had reddish staining cytoplasm and a large nucleus; macrogametocytes had a bluish cytoplasm and a compact nucleus. Both had coarse black pigment.

Experimental

Laboratory-bred mosquitoes (*Culex fatigans* Wiedemann) were allowed to feed on a *V. pumilis* with scanty gametocytes in its blood. From 16 to 21 days later the mosquitoes were dissected but no evidence of development was found in 21 examined.

Life History

The most important advance in our knowledge of these parasites of small bats was made by Goldblum in Israel, who found minute schizonts in fixed and wandering macrophages and in cells of the myeloid series. Schizogony occurred in the bone marrow, spleen, lungs, kidneys, and liver. The same author found oocysts and sporozoites in two species of nycteribiid flies, *Penicillidia dufouri* and *P. conspicua* (Goldblum 1951).

Genus BABESIA Starcovici

Babesia sp.

Backhouse and Bolliger (1957) reported the presence of large fusiform bodies, suggestive of the genus *Babesia*, in the red cells of an echidna, *Tachyglossus aculeatus*, from Moss Vale, N.S.W. The parasites were most readily found in smears of the vertebral bone marrow, 2, 4, or 8 parasites being present in some cells. *Theileria tachyglossi* was present in the same animal. Dr. Backhouse kindly sent me a slide from this echidna, which showed parasites resembling in a general way those described below as *Babesia thylacis*.

Babesia thylacis, sp. nov.

Host.—*Thylacis obesulus* (Shaw).

Distribution.—Brisbane, Innisfail, Qld.

Type.—Slide from *T. obesulus* from Brisbane in the Queensland Museum, Brisbane.

A scanty infection was found in an adult male bandicoot captured near Brisbane, and three young bandicoots were infected by progressive subinoculation from it. Parasites were also found in small numbers in a blood film from a bandicoot from Innisfail. The infection rate is probably higher than these observations would suggest. The short period of patency and low density of parasitaemia could lead to many infections being missed.

Morphology (*Plate* 4, *Figs.* 11–14)

The youngest stages seen were small amoeboid organisms. The fully grown parasites were fusiform or pear-shaped, 3–5 μ by 1·5 μ; cytoplasm usually containing a vacuole; nucleus sometimes rounded and terminal in position, sometimes rather elongate and stretched out along the periphery of the organism. Cells containing 1 or 2 young parasites did not appear to be altered, but those containing 2, 4, or 8 fully developed parasites were definitely enlarged and paler than normal.

Experimental

Three young animals were successively inoculated intraperitoneally with citrated blood containing parasites. The infection became patent on the 3rd day in two animals, and on the 5th in the other. Parasites were never numerous in the peripheral blood, and disappeared after a few days. The animals showed no signs of illness. An adult bandicoot, inoculated on two occasions with blood containing *Babesia*, showed a single infected red cell on one occasion. It did not relapse after splenectomy.

The Babesias of Cattle

Pathogenic organisms causing redwater fever in cattle were first recognized by Pound (1895) and Hunt and Collins (1896) in the blood of animals suffering from the disease in the Gulf country of Queensland. It gradually became apparent that more than one species was present, and in 1935 Legg showed that *Babesia argentina* was definitely present as well as *B. bigemina*.

Both these organisms were probably introduced into the Northern Territory when 12 tick-infested Brahmin cattle were brought to Darwin from Java in 1872. The cattle tick and its associated parasites have now become distributed over a wide belt of country from the Kimberleys in Western Australia through the Northern Territory and coastal Queensland to the north-eastern corner of New South Wales. A full account of the history, clinical effects, pathology, treatment, and economic aspects of babesiosis will be found in Seddon (1952). The classification and biology of the group have been dealt with by Neitz (1956).

Babesia bigemina (Smith & Kilborne)

These are small, amoeboid, irregular, or pear-shaped parasites, about 3–4 μ in length. The most characteristic appearance is seen when two pear-shaped bodies lie close together in a cell (Plate 4, Figs. 15–17).

Dennis (1931) worked out the details of the development of *B. bigemina* in the tick, *Boophilus annulatus* (Say), in North America. No one has yet found the corresponding stages in *B. microplus* (Canestrini) in Australia, but it is well known that the progeny of infected female ticks can transmit the infection to clean animals.

Babesia argentina (Lignières)

These are small ring-shaped, or elliptical parasites, about 2·5 μ in length or less. When two occur in a cell, they usually diverge widely from each other (Plate 4, Figs. 18 and 19). These organisms may be very scanty in the peripheral blood, but are usually more numerous in kidney smears.

This species is transmitted by *B. microplus*, but the details of the development in the tick are not known.

Genus THEILERIA Bettencourt, França, & Borges

Neitz (1956) placed the parasite of the echidna, *Theileria tachyglossi* Priestley, in the genus *Gonderia* along with the non-pathogenic *Th. mutans* of cattle, restricting the generic name *Theileria* to a single species, *Th. parva*. This classification may eventually be adopted, but in this work the generic name *Theileria* is used in a wide sense for the small, pleomorphic, non-pigmented parasites of red cells, the schizogonic stages and life histories of which are imperfectly known.

Theileria tachyglossi Priestley

Theileria tachyglossi Priestley, 1915, p. 233.

Host.—*Tachyglossus aculeatus* (Shaw).

Distribution.—Townsville (type locality), N. Qld.; Maleny, Brisbane, S. Qld.; Moss Vale, Glen Davis, N.S.W.

Morphology (*Plate* 5, *Figs.* 1–4)

Priestley (1915) described bacilliform, comma-shaped, ovoid, pyriform, and rounded forms. Multiple infection of red cells was rare in his films. Koch's bodies were found in small numbers in the peripheral blood, but were numerous in organ smears. The author considered that schizogony occurred in leucocytes.

Backhouse and Bolliger (1957) reported the results of examining 12 echidnas which had died in the Taronga Park Zoological Gardens, Sydney. Nine were infected with *Th. tachyglossi*. These authors attempted unsuccessfully to transmit the parasite to rats, mice, and possums (*Trichosurus vulpecula*) by injecting blood, spleen pulp, and bone marrow. They did not find Koch's bodies in spleen smears.

Films have been examined from 6 echidnas, 2 from Glen Davis, and 4 from south Queensland. Parasites were present in 5 animals, being moderately numerous in 3, scanty in the others. Usually only 1 parasite was found in a red cell, but 2, 3, and 4 were very occasionally seen. Slender bacillary forms were most frequent but appliqué forms were quite readily found in 1 animal (Fig. 2).

Through the courtesy of Dr. T. C. Backhouse, School of Public Health and Tropical Medicine, Sydney, I have been privileged to examine the original organ smears made by Priestley in 1913. The spleen smear, though considerably faded, shows bodies which are presumably schizonts in leucocytes (Fig. 4). The life history is unknown.

Theileria ornithorhynchi, sp. nov.

Host.—Ornithorhynchus anatinus (Shaw).

Distribution.—Interlaken, Tas.; Upper Brookfield (near Brisbane), Innisfail.

Type.—Slide from *O. anatinus* from Upper Brookfield in the Queensland Museum, Brisbane.

Dr. Duncan observed these parasites in the platypus from Interlaken in 1950, and they were present in both animals examined in Queensland.

Morphology (*Plate* 5, *Figs.* 5–6)

Minute, rounded, oval, or elongate parasites with nucleus usually near one end. Single parasites were found to predominate in the infection from Upper Brookfield, but very rarely 2, 3, or 4 were present in a cell. Multiple infections were more readily found in the films from Innisfail, as many as 6 parasites being seen in some cells. These were smaller than those in singly infected cells, being minute, ovoid, or rod-like bodies with tiny terminal nuclei (Fig. 6). No schizonts were detected in films nor in sections of liver, spleen, and lung, which were obtained from one platypus.

The relationship of this parasite to *Th. tachyglossi* remains to be determined. Species of *Theileria* resemble one another closely, and they also vary in appearance in films from different animals of the same species, slender forms predominating in some films, ovoid forms in others. It is risky, therefore, to attempt to define morphological differences. The hosts, however, occupy very different ecological niches, and have different ectoparasites, the tick, *Ixodes ornithorhynchi* Lucas, being peculiar to the platypus, whereas the echidna is frequently infested with *Aponomma decorosum* Koch and *A. hydrosauri* Denny. The life history is unknown.

Theileria peramelis, sp. nov.

Theileria sp., Mackerras, Mackerras, and Sandars, 1953, p. 61.

Hosts.—Thylacis obesulus (Shaw), *Perameles nasuta* Geoffroy, and *Potorous tridactylus* (Kerr).

Distribution.—Brisbane, Mt. Nebo, S. Qld.

Type.—Slide from *T. obesulus* from Brisbane in the Queensland Museum, Brisbane.

We have seen two infections in *P. nasuta*, and numerous others in *T. obesulus*. Usually only a scanty infection was present, but a few animals showed moderately numerous organisms.

Morphology (*Plate* 5, *Figs.* 7–8)

Minute, oval, or pear-shaped bodies, occasionally rod-like. Appliqué forms were sometimes seen. Usually only one parasite was seen in a red cell during the chronic phase, but pairs were found quite frequently during the height of the infection. The division of a single organism into two seemed to follow a definite plan. The nucleus, which lay at the blunt end of the parasite, divided first and then division of the cytoplasm occurred from this end, so that a stage was reached when the members of the pair were still united at their pointed ends. When division was complete the pointed ends swung away from each other, so that the two organisms came to lie almost in a straight line, with the blunt (nucleated) ends near each other, and the pointed ends directed towards the periphery of the cell. This characteristic appearance was often noted (Fig. 7). Cross forms were not observed. Koch's bodies were not found.

In thick films stained by Field's method, the parasites were very uniform in size, appearing as minute blue rings or disks, with a dark red nucleus at the periphery.

Infected cells were usually small mature erythrocytes. Reticulocytes were common in most films, but it was exceptional to find one infected. There must be considerable blood destruction, as signs of anaemia were seen in many infected bandicoots, marked anisocytosis, polychromasia, and the occurrence of nucleated red cells in the circulation being frequently noted. Four large polychromasic cells are seen in Figure 8. The animals, however, showed no other indications of illness.

Sections and organs smears from two moderately infected animals, and sections from 14 others with scanty infections were searched, but no unequivocal schizonts were found.

The parasites seen in films from a rat-kangaroo, *Potorous tridactylus*, have been tentatively assigned to this species. They are slightly larger on the average than forms in bandicoots, but otherwise appear similar morphologically (Plate 5, Fig. 9). The hosts occupy similar ecological niches, and certain fleas are found on both. It seems likely that the ticks which attack bandicoots would also attack rat-kangaroos.

Experimental

Infection was transmitted to other bandicoots by the intraperitoneal injection of citrated blood or organ emulsion, and its course in two animals, which had been reared from the pouch young state in the laboratory, was as follows: Parasites appeared 21 and 28 days after inoculation. At first they were very scanty, but gradually increased in numbers, so that by the 6th and 7th week they were fairly numerous. By this time the blood showed signs of anaemia; it was paler than normal and microscopically showed anisocytosis and polychromasia. Nucleated red cells were

frequently seen. Parasites then began to diminish in numbers, and the blood picture to improve. Scanty parasites were still present 11 weeks and 13 weeks after infection.

A similar sequence of events was observed in two naturally infected bandicoots. One developed a parasite wave spontaneously 2 weeks after capture, and the other relapsed after splenectomy. In the former, the slow rise in parasite numbers, the development of anaemia, and the prolonged chronic phase, with scanty parasites constantly present, was exactly similar to what has been described for the course of infection following artificial inoculation. The splenectomized animal had scanty parasites at the time of operation. Twelve days later, they began to increase and the course of infection followed that described above. Two months after operation, the blood picture had returned to normal but parasites were still present in small numbers.

Life History

Unknown. One of the ticks commonly found on bandicoots will probably be incriminated. These include 3 species of *Ixodes* and 1 of *Haemaphysalis*.

Theileria mutans (Theiler)

This parasite of cattle was first recognized in Australia by Dodd in 1910, and recorded by him in 1923. It is smaller than either *Babesia bigemina* or *B. argentina*, but forms occur which cannot be separated with certainty from young babesias. Narrowly oval or slender, rod-shaped forms occur, sometimes the latter stretching right across the red cell (Plate 5, Figs. 10 and 11). It does not usually cause morbidity but may produce a severe illness in splenectomized animals. It is transmitted by the cattle tick, *Boophilus microplus*, but, because it occurs in areas free from cattle ticks, it must have another vector and *Haemaphysalis bispinosa* Neumann has been suspected of transmitting it (Roberts 1952).

VI. Miscellaneous Parasites

Genus ANAPLASMA Theiler

Two species are known in Australia, both being parasites of cattle. They are minute coccoid bodies contained in red cells.

The first light on the mode of reproduction of these organisms was thrown by de Robertis and Epstein (1951), who showed by electron microscopy that the apparently single round bodies might consist of a large number of submicroscopic particles. This work has been confirmed by Foote, Geer, and Stich (1958), who examined by electron microscopy sections of infected red cells cut at 0·05–0·025 μ. The anaplasma body was seen as a clear space containing 1–7 dense masses. They considered that the appearance of the organism supported the idea that it is a virus.

Anaplasma marginale Theiler

Legg recognized *A. marginale* in the red cells of cattle at Townsville in 1933. It was probably introduced at the same time as its vector, the cattle tick, *Boophilus microplus*, along with other associated parasites, but it remained unrecognized for

many years. Its manifestations had been regarded as relapses to babesiosis because of its longer incubation period. It causes a severe illness with fever and anaemia.

Morphologically, the organisms appear as minute, round, deeply staining dots, the majority (but not all) lying at or near the margin of the red cell (Plate 6, Fig. 1). They vary in size, reaching about $0 \cdot 5\ \mu$ in diameter.

Anaplasma centrale Theiler

This organism resembles the preceding, but occurs characteristically near the centre of the cell (Plate 6, Fig. 2). It is less virulent than *A. marginale*. It was introduced into Australia by Dr. J. A. Gilruth to provide a means of protecting cattle against *A. marginale*, because it had been found in South Africa that animals infected with *A. centrale* acquired considerable resistance to subsequent infection with *A. marginale*.

Genus HAEMOBARTONELLA Tyzzer & Weinman

The bartonellas have been divided into two groups, the generic name *Bartonella* being used for the human pathogen (*B. bacilliformis*) which multiplies in endothelial cells as well as red cells and causes cutaneous lesions, and *Haemobartonella* for those organisms which apparently only multiply in red cells and which do not cause skin lesions. *B. bacilliformis* is readily cultivated *in vitro*; it possesses numerous long flagella, well seen by electron-microscopy.

Haemobartonella muris (Mayer)

The parasites appear in Giemsa-stained blood films of rats as very short slender rods lying in or on the red cells (Plate 6, Figs. 4 and 5). Wigand and Peters (1952) have shown by electron-microscopy that the rods are composed of chains of minute spheres. They grow slowly on various blood media, only minute colonies being present after 48 hr (Wilson and Miles 1955). Only an occasional parasitized cell is seen in normal animals but the numbers may increase greatly after splenectomy. A severe anaemia, with haemoglobinuria which is sometimes fatal, occurs. Transmission in nature is said to be by lice.

This species has been recorded in laboratory rats in Sydney by Black (1951), and in *Rattus villosissimus* Waite from north-western Queensland by Pope and Carley (1956). It has been seen in laboratory rats in Brisbane. and in several native rats from Innisfail. It was found in 6 out of 38 *Rattus assimilis* (Gould), in 17 out of 80 *Melomys littoralis* Lönnberg, and in 2 out of 37 *Hydromys chrysogaster* Geoffroy.

Haemobartonella bovis (Donatien & Lestoquard)

The organisms occur in the red cells of cattle, and resemble *H. muris* in morphology. Mulhearn found them in 1944 in animals undergoing immunization for babesiosis at Townsville (Mulhearn 1946). The parasites were only seen for a few days. Infection has also been found in a Victorian calf (Seddon 1953), so that its distribution is wider than that of the cattle tick.

? Haemobartonella sp.

Organisms have been seen in very scanty numbers in two bandicoots, *Thylacis obesulus*, from Brisbane. They resembled *H. muris* but were thinner and more spaced out in the red cell (Plate 6, Fig. 6). They may belong to this genus or to *Grahamella* Brumpt.

Genus EPERYTHROZOON Schilling

Eperythrozoon coccoides Schilling

Minute, coccoid bodies, often with paler centres, so that they appear as rings 1–2 μ in diameter. They adhere to the surface of the red cells of mice or lie free in the plasma. The free forms stain rather palely with Giemsa, but those adherent to red cells take a more intense stain. They have not been grown *in vitro*. They cause a chronic anaemia.

Derrick *et al.* (1954) studied the infection in laboratory mice in Brisbane. A high titre of infectivity was found in the blood 14 days after inoculation, although the organisms could rarely be detected in films. After splenectomy, however, enormous numbers of organisms appeared in the blood. The infection was self-limited, terminating naturally after 12–21 weeks. Infected cells were usually large and polychromasic (Plate 6, Fig. 3).

Transmission by lice, *Polyplax serrata* (Burmeister), has been recorded in other parts of the world. Electron-microscopy failed to reveal any internal structure or cell membrane (Peters and Wigand 1955). These authors consider that the parasite is closely related to *Haemobartonella muris*.

Eperythrozoon wenyoni Adler & Ellenbogen

The organisms occur in the blood of cattle. They are rarely seen and then only in splenectomized animals. They resemble *E. coccoides* in morphology. They were seen by Mulhearn in Queensland cattle in 1949 (personal communication) and recorded by Seddon (1953).

Genus BORRELIA Swellengrebel

Spirochaetes with shallow irregular spirals, tapering terminally. They measure from 8 to 16 μ in length. They are found in the blood and are usually stained readily by Romanowsky methods.

Borrelia theileri (Laveran)

These large spirochaetes have been reported in the blood of cattle in Queensland (Mulhearn 1946), and Roberts (1952) considers that they are probably transmitted by the cattle tick, *Boophilus microplus*. Carley and Pope (1958) inoculated blood from four calves, all showing *B. theileri*, into laboratory rats and mice but no spirochaetes could be detected in any of the recipients.

Borrelia sp.

Pope and Carley (1956) isolated a species of *Borrelia* from native rats, *Rattus villosissimus* Waite, which had reached plague proportions in north-western Queensland. It has been maintained in laboratory mice in which it produces an acute infection, the spirochaetes reaching a density of 6,000–17,000 per cu.mm on the 3rd or 4th day after inoculation, and then declining rapidly. Attemps to infect a human volunteer were unsuccessful (Carley and Pope 1957). Attempts to transmit the infection from mouse to mouse by the argasid tick, *Ornithodorus gurneyi* Warburton, were also unsuccessful (Carley and Pope 1958).

Borrelia sp.

Spirochaetes have been found in blood films of three bandicoots, *Thylacis obesulus*, taken near Brisbane. These were large organisms of typical appearance (Plate 6, Fig. 7). An attempt to infect laboratory mice with them was unsuccessful.

Borrelia sp.

Spirochaetes, which varied a good deal in size, were found in blood films from kangaroos taken in western Queensland by Messrs. J. H. Pope and A. J. Carroll. They were present in 2 out of 72 *Macropus major* Shaw, and in 2 out of 50 *M. rufus* (Desmarest). The infected animals came from Augathella, Blackall, and Muckadilla (Plate 6, Fig. 8).

Inoculation of blood clot into laboratory mice, one young bandicoot (*Thylacis obesulus*), and one young possum (*Trichosurus vulpecula* (Kerr)) failed to produce an infection in any of the recipients (J. H. Pope, unpublished data).

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VIII. References

Backhouse, T. C., and Bolliger, A. (1957).—A piroplasm of the echidna (*Tachyglossus aculeatus*). *Aust. J. Sci.* **20**: 24–5.

Balfour, A. (1905).—A haemogregarine of mammals—*H. jaculi*, *H. balfouri* (Laveran). *J. Trop. Med.* **8**: 241–4.

Balfour, A. (1906).—A haemogregarine of mammals. Second Rep. Wellcome Trop. Res. Lab. pp. 97–112.

Bancroft, T. L. (1888).—Note on Haematomonas in rats' blood. *Proc. Roy. Soc. Qd.* **5**: 31 2.

Bauer, F. von, and Hohorst, W. (1958).—*Hepatocystis kochi*. *Acta Trop.* **15**: 169–73.

Bearup, A. J., and Lawrence, J. J. (1947).—A search for the vector of *Plasmodium pteropi* Breinl. *Proc. Linn. Soc. N.S.W.* **71**: 197–200.

Black, R. H. (1951).—The effect of neoarsphenamine on *Plasmodium berghei* infections in the mouse and rat: inhibition of anti-malarial action of neoarsphenamine by British anti-lewisite. *Ann. Trop. Med. Parasit.* **45**: 127–36.

Breinl, A. (1913).—Parasitic protozoa encountered in the blood of Australian native animals. Rep. Aust. Inst. Trop. Med. for 1911. pp. 30–8.

Bull, L. B. (1914).—Tuberculosis in dogs. *Vet. J.* **70**: 34–44.

Carley, J. G., and Pope, J. H. (1957).—Studies of *Borrelia*. Twelfth Ann. Rep. Qd. Inst. Med. Res. for 1957. pp. 5–6.

Carley, J. G., and Pope, J. H. (1958).—Studies of *Borrelia*. Thirteenth Ann. Rep. Qd. Inst. Med. Res. for 1958. p. 4.

Christophers, S. R. (1905).—*Haemogregarina gerbilli*. Sci. Mem. Med. Sanit. Dep. India. No. 18. pp. 1–15.

Cleland, J. B. (1906).—The haemogregarine of mammals (*H. balfouri*), and some notes on rats. *J. Trop. Med.* **9**: 296–7.

Cleland, J. B. (1908).—Some remarks on the natural history and disease of the rats of Perth and Fremantle, Western Australia. Rep. Aust. Ass. Advanc. Sci. for 1907. pp. 516–20.

Cleland, J. B. (1909).—Trypanosomiasis and other diseases in camels, with experiments in connection with the former. Aust. Med. Congr. for 1908. Vol. 2. pp. 305–24.

Dennis, E. W. (1931).—The life history of *Babesia bigemina* in the North American fever tick. *Science* **73**: 620–1.

Derrick, E. H., Pope, J. H., Chong, S. K., Carley, J. G., and Lee, P. E. (1954). Observations on infections of mice with *Eperythrozoon coccoides* Schilling. *Aust. J. Exp. Biol. Med. Sci.* **32**: 577–82.

Dodd, S. (1910).—Diseases in stock. Ann. Rep. Dep. Agric. Qd. for 1909–10. pp. 19–22.

Dodd, S. (1924).—The pirpolasmoses of the Pacific Regions. Proc. Pan-Pacific Sci. Congr. for 1923. pp. 1502–12.

Flu, P. C. (1908).—Über die Flagellaten im Darm von *Melophagus ovinus*. *Arch. Protistenk.* **12**: 147–53.

Foote, L. E., Geer, J. C., and Stich, Y. E. (1958).—Electron-microscopy of the Anaplasma body: ultra-thin sections of bovine erythrocytes. *Science* **128**: 147–8.

Garnham, P. C. C. (1951). An attempt to find the vector of *Hepatocystis* (= *Plasmodium*) *kochi* (Levaditi and Schoen). *Exp. Parasit.* **1**: 94–107.

Garnham, P. C. C. (1957). Trees, ticks and monkeys: further attempts to discover the invertebrate host of *Hepatocystis kochi*. *Z. Tropenmed. u. Parasit.* **8**: 91–6.

Garnham, P. C. C., and Lewis, D. J. (1958).—Demonstration. Some parasites from British Honduras. *Trans. Roy. Soc. Trop. Med. Hyg.* **52**: 295–6.

Goldblum, N. (1951).—Studies on Haemosporidiidea, parasites of bats in Israel. Ph.D. Thesis, Hebrew University, Jerusalem.

Hoare, C. A. (1932).—On protozoal blood parasites collected in Uganda. With an account of the life cycle of the crocodile haemogregarine. *Parasitology* **24**: 210–24.

Hoare, C. A. (1949).—"Handbook of Medical Protozoology." (Baillière, Tindall & Cox: London.)

Hunt, J. S., and Collins, W. (1896).—Report on tick fever. Report of Special Commission, Brisbane, 1896.

JOHNSTON, T. H. (1909).—Notes and exhibits. *Proc. Linn. Soc. N.S.W.* **34**: 218.

KENT, W. S. (1880–1).—"A Manual of the Infusoria." Vol. 1. (David Bogue: London.)

KUDO, R. R. (1946).—"Protozoology." (Charles C. Thomas: Springfield, Ill.)

LAVERAN, A. (1902).—Sur un nouveau Trypanosome des Bovidés. *C.R. Acad. Sci., Paris* **134**: 512–14.

LAWRENCE, J. J. (1955).—The asexual multiplication of the 'malaria parasite' of Australian flying foxes. *Aust. J. Sci.* **18**: 61–2.

LEGER, M., and BAURY, A. (1923).—Trypanosome de la chauve-souris du Sénégal, *Hipposiderus tridens* Et. Geoff. *C.R. Soc. Biol., Paris* **88**: 866–9.

LEGG, J. (1933).—The occurrence of *Anaplasma marginale* Theiler, 1910 in northern Queensland. Pamphl. Coun. Sci. Industr. Res. Aust. No. 38.

LEGG, J. (1935).—The occurrence of bovine babesiellosis in northern Queensland. Pamphl. Coun. Sci. Industr. Res. Aust. No. 56.

MACKERRAS, I. M., MACKERRAS, M. J., and SANDARS, D. F. (1953).—Parasites of the bandicoot, *Isoodon obesulus*. *Proc. Roy. Soc. Qd.* **63**: 61–3.

MANWELL, R. D. (1946).—Bat malaria. *Amer. J. Hyg.* **43**: 1–12.

MULHEARN, C. R. (1946).—A note on two blood parasites of cattle (*Spirochaeta theileri* and *Bartonella bovis*) recorded for the first time in Australia. *Aust. Vet. J.* **22**: 118–19.

NEITZ, W. O. (1956).—Classification, transmission, and biology of piroplasms of domestic animals. *Ann. N.Y. Acad. Sci.* **64**: 56–111.

NÖLLER, W. (1925).—Der Nachweis des Überträgers des gemeinen Rindertrypanosomas, *Trypanosoma theileri*, mit Hilfe des Kulturverfahrens. *Zbl. Bakt.* (1 *Abt. Ref.*) **79**: 133–42.

O'BRIEN, R. A. (1909).—Ankylostomiasis and other tropical diseases in Queensland. Aust. Med. Congr. for 1908. Vol. 2. pp. 324–8.

OWEN, W. J. (undated).—*Trypanosoma* in the monotreme. Publ. Aust. Inst. Anat., Canberra. (Commonw. Govt. Printer: Canberra.)

PETERS, D., and WIGAND, R. (1955).—Bartonellaceae. *Bact. Rev.* **19**: 150–5.

POPE, J. H., and CARLEY, J. G. (1956).—Isolation of *Borrelia* from native rats in north-west Queensland. *Aust. J. Sci.* **19**: 114.

POUND, C. J. (1895).—Redwater disease in cattle in the Gulf district. (Govt. Printer: Brisbane.)

POUND, C. J. (1905).—On *Trypanosoma* and their presence in the blood of Brisbane rats. *Proc. Roy. Soc. Qd.* **19**: 33–8.

PRIESTLEY, H. (1915).—*Theileria tachyglossi* (n.sp.). A blood parasite of *Tachyglossus aculeatus*. *Ann. Trop. Med. Parasit.* **9**: 233–8.

ROBERTIS, E. DE, and EPSTEIN, B. (1951).—Electron microscope study of anaplasmosis in bovine red blood cells. *Proc. Soc. Exp. Biol., N.Y.* **77**: 254–8.

ROBERTS, F. H. S. (1952).—"Insects Affecting Livestock." (Angus & Robertson Ltd.: Sydney.)

RODHAIN, J. (1951).—*Trypanosoma leleupi* n.sp., parasite de *Hipposideros caffer* au Katanga. *Ann. Parasit. Hum. Comp.* **26**: 133–7.

SEDDON, H. R. (1952).—Diseases of domestic animals in Australia. Pt. 4. Protozoan and viral diseases. Serv. Publ. Dep. Hlth. Aust. Vet. Hyg. No. 8. 214 pp.

SEDDON, H. R. (1953).—Diseases of domestic animals in Australia. Pt. 5. Vol. 2. Bacterial diseases. Serv. Publ. Dep. Hlth. Aust. Vet. Hyg. No. 10. 464 pp.

TURNER, A. W., and MURNANE, D. (1930).—Trypanosomes in the blood of Victorian animals. 1. A preliminary note on the occurrence of *Trypanosoma theileri* in the blood of cattle. 2. On the presence of *Trypanosoma melophagium* in the blood of Victorian sheep, and its transmission by the sheep "tick", *Melophagus ovinus*. *J. Coun. Sci. Industr. Res. Aust.* **3**: 120–2.

D'UTRA, O., SILVA, A., and ARANTES, J. B. (1917).—Sobre uma hemogregarina da gambá. *Haemogregarina didelphydis* n.sp. *Mem. Inst. Osw. Cruz.* **8**: 61–3.

WELSH, D. A., and BARLING, J. E. V. (1909).—*Haemogregarina petauri*: a haemogregarine of a marsupial flying squirrel. Aust. Med. Congr. for 1908. Vol. 2. pp. 329–33.

WELSH, D. A., and BARLING, J. E. V. (1910).—*Haemogregarina petauri*: a haemogregarine of a marsupial flying squirrel. *J. Path. Bact.* **14**: 536–41.

Welsh, D. A., and Dalyell, E. J. (1909).—*Haemogregarina peramelis*: a free haemogregarine of an Australian bandicoot. *J. Univ. Sydney Med. Soc.* (N.S.)**1909**(2): 112–15.

Welsh, D. A., and Dalyell, E. J. (1910).—*Haemogregarina peramelis*: a free haemogregarine of an Australian bandicoot. *J. Path. Bact.* **14**: 547–9.

Welsh, D. A., Dalyell, E. J., and Burfitt, M. B. (1909).—*Haemogregarina dasyuri*. A preliminary note on an undescribed haemogregarine of the Australian native cat. Aust. Med. Congr. for 1908. Vol. 2. pp. 333–7.

Welsh, D. A., Dalyell, E. J., and Burfitt, M. B. (1910).—*Haemogregarina dasyuri*: a haemogregarine of the Australian native cat. *J. Path. Bact.* **14**: 542–6.

Wenyon, C. M. (1926).—"Protozoology." (Baillière, Tindall, & Cox: London.)

Wigand, R., and Peters, D. (1952).—Neuere Untersuchungen über *Bartonella muris* Mayer. *Z. Tropenmed. u. Parasit.* **3**: 437–52.

Wilson, G. S., and Miles, A. A. (1955).—"Principles of Bacteriology and Immunity." 4th Ed. (Edward Arnold & Co.: London.)

Explanation of Plates 1–6

With the exceptions of Plate 1, Figure 1, Plate 2, Figures 9 and 10, and Plate 4, Figures 1 and 2, all photomicrographs were taken at the same magnification with a Leitz Panphot microscope, using a ×8 periplan eyepiece and a 2-mm apochromatic oil-immersion objective

Plate 1

Figure 1 is a photomicrograph taken by Dr. C. A. Duncan. *F*, free flagellum; *K*, kinetoplast; *N*, nucleus

Figs. 1–3.—*Trypanosoma binneyi* in the blood of *Ornithorhynchus anatinus*.

Figs. 4–6.—*T. thylacis* in the blood of *Thylacis obesulus*.

Fig. 7.—Trypanosome from the subcutaneous tissue of *T. obesulus*.

Figs. 8–10.—Flagellates in culture from spleen of *T. obesulus*.

Fig. 11.—Trypanosome in *Ixodes holocyclus* nymph.

Plate 2

Figures 9 and 10 are from Turner and Murnane (1930)

Fig. 1.—*Trypanosoma lewisi* in the blood of *Rattus norvegicus* during the phase of multiplication.

Fig. 2.—*T. lewisi* in the blood of *R. norvegicus* during the chronic phase.

Figs. 3–5.—*T. pteropi* in the blood of *Pteropus* sp.

Figs. 6–8.—*T. hipposideri* in the blood of *Hipposideros bicolor albanensis*.

Fig. 9.—*T. theileri* in the blood of an ox.

Fig. 10.—*T. melophagium* in the blood of a lamb.

Plate 3

Figs. 1 and 2.—*Hepatozoon muris* in the monocytes of *Rattus assimilis*.

Fig. 3.—*H. muris* schizont in liver of *R. norvegicus*.

Figs. 4–6.—*H. petauri* in the blood of *Petaurus breviceps*.

Figs. 7 and 8.—*Hepatozoon* sp. in the blood of *P. breviceps*.

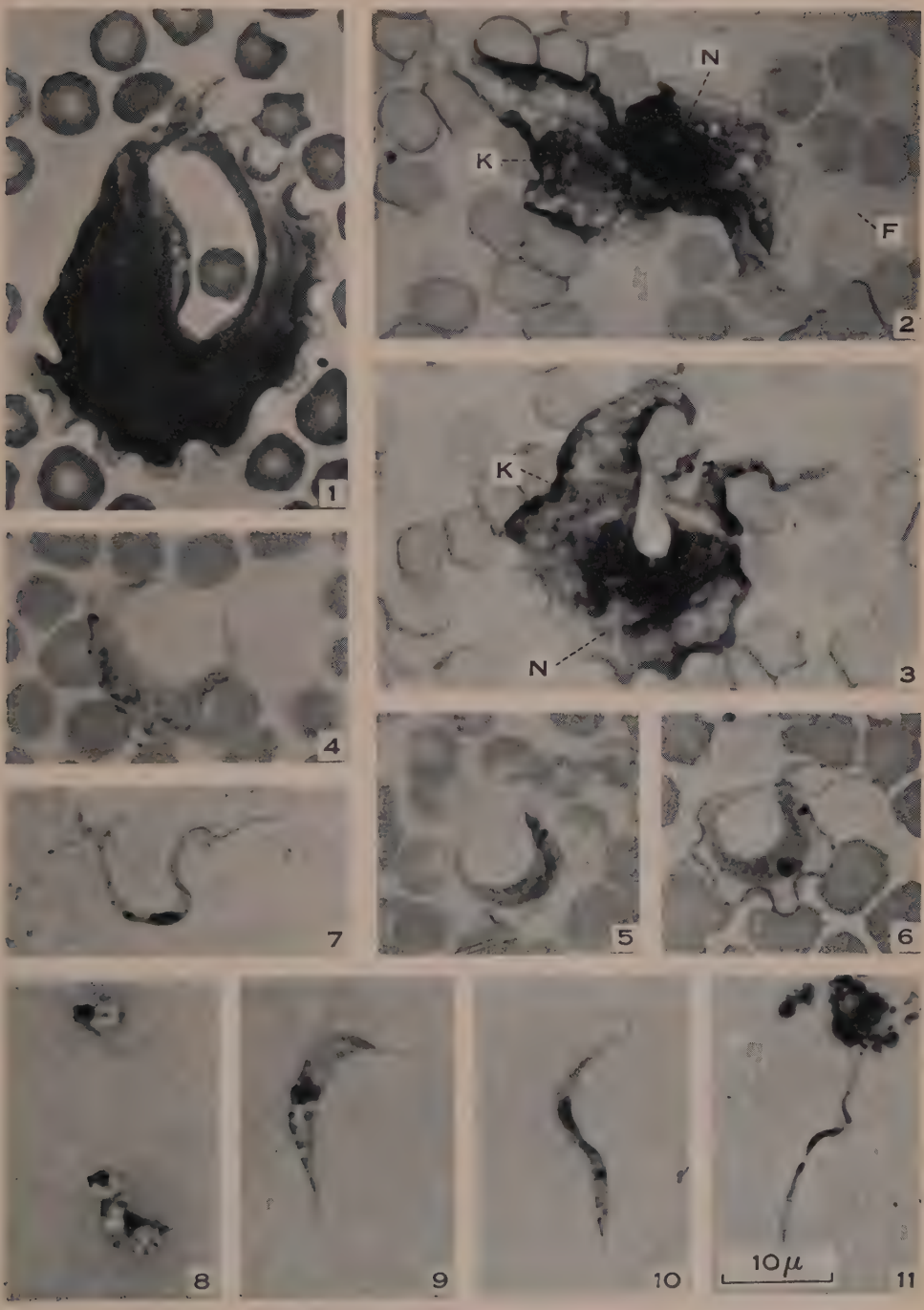
Figs. 9 and 10—*H. pseudocheiri* in the blood of *Pseudocheirus laniginosus*.

Fig. 11.—*H. pseudocheiri*, free vermicule in the blood of *P. laniginosus*.

Figs. 12–14.—*H. dasyuroides* in the blood of *Dasyuroides byrnei*.

Figs. 15–17.—*H. peramelis* in the blood of *Thylacis obesulus*.

THE HAEMATOZOA OF AUSTRALIAN MAMMALS



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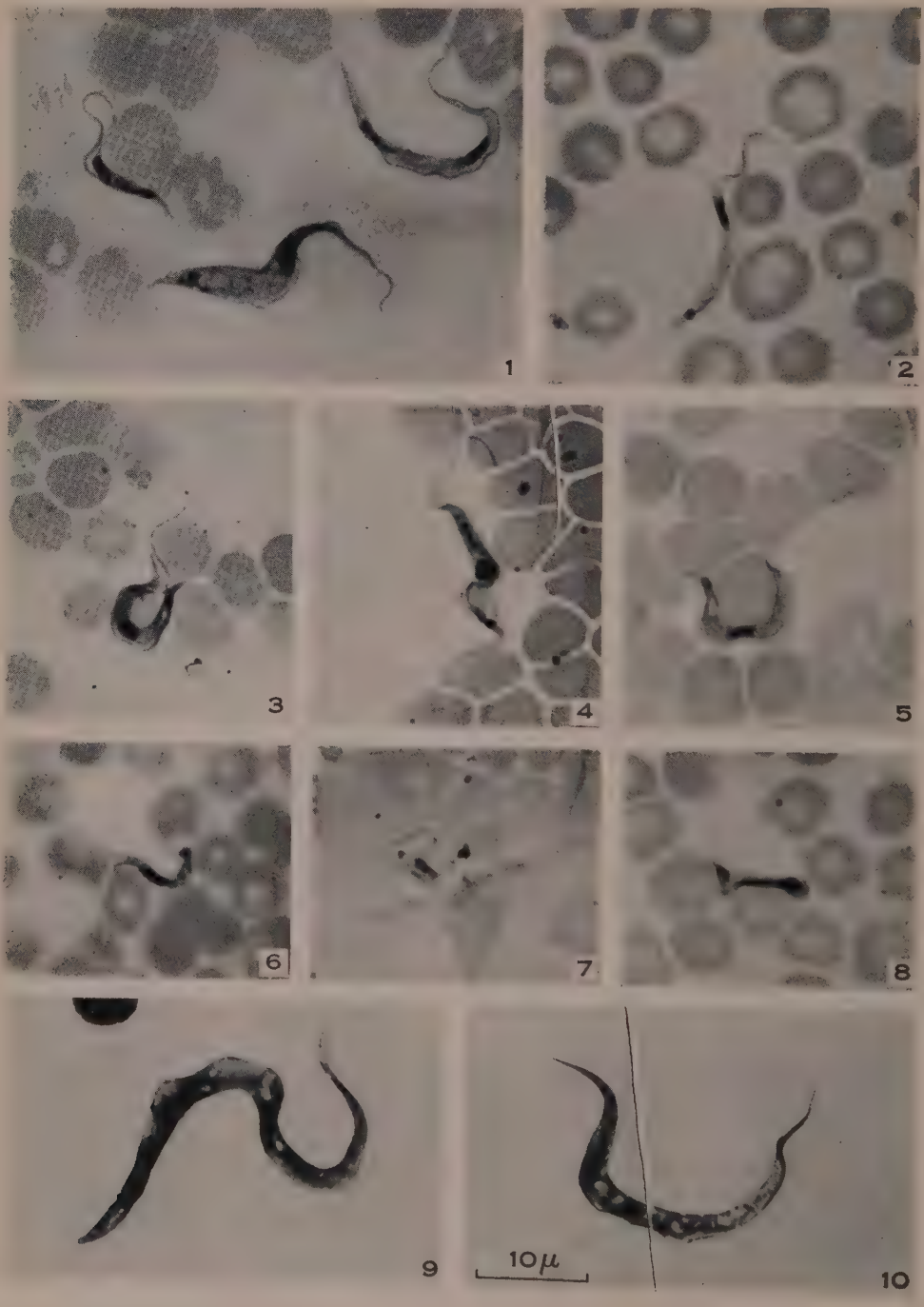

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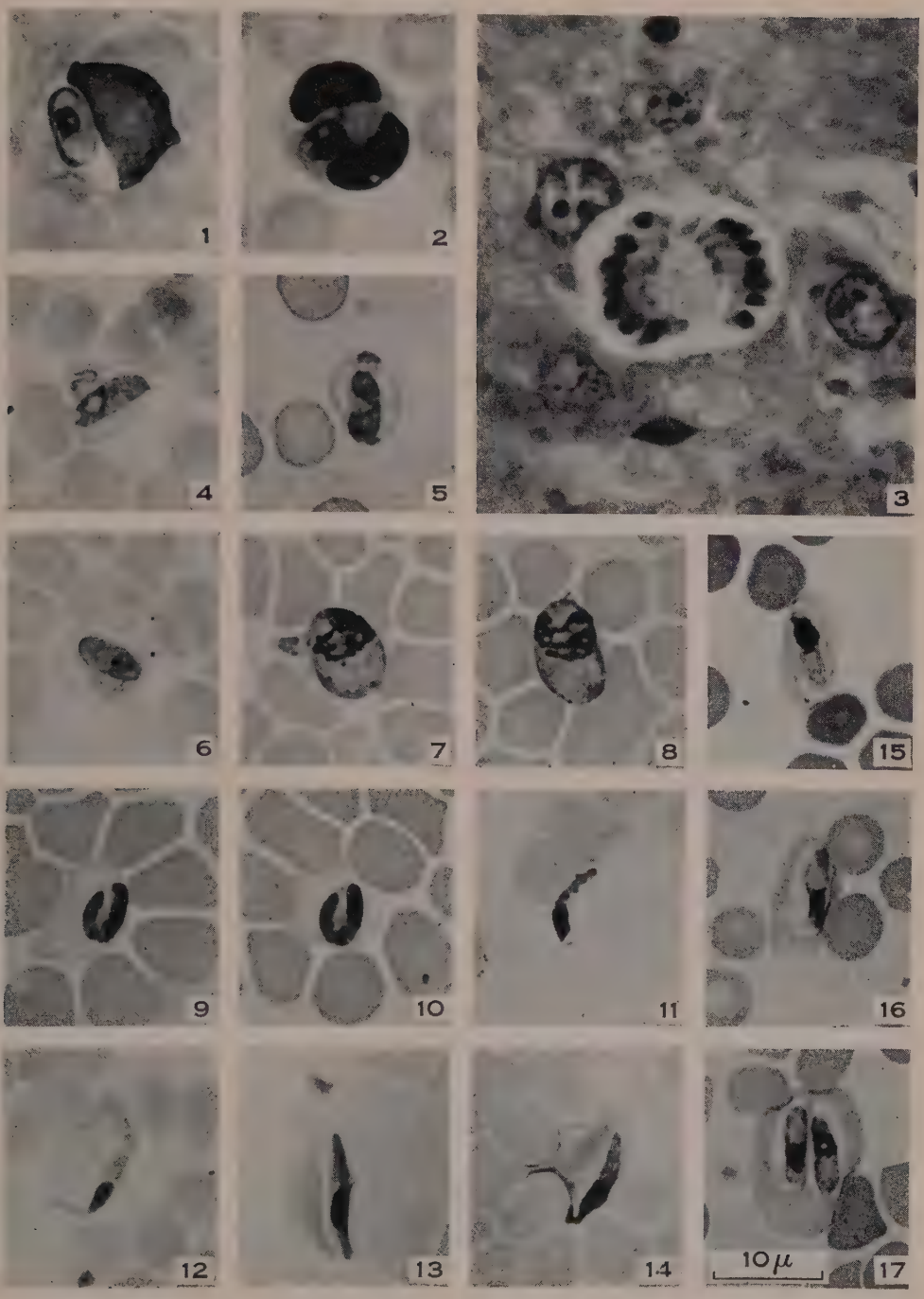

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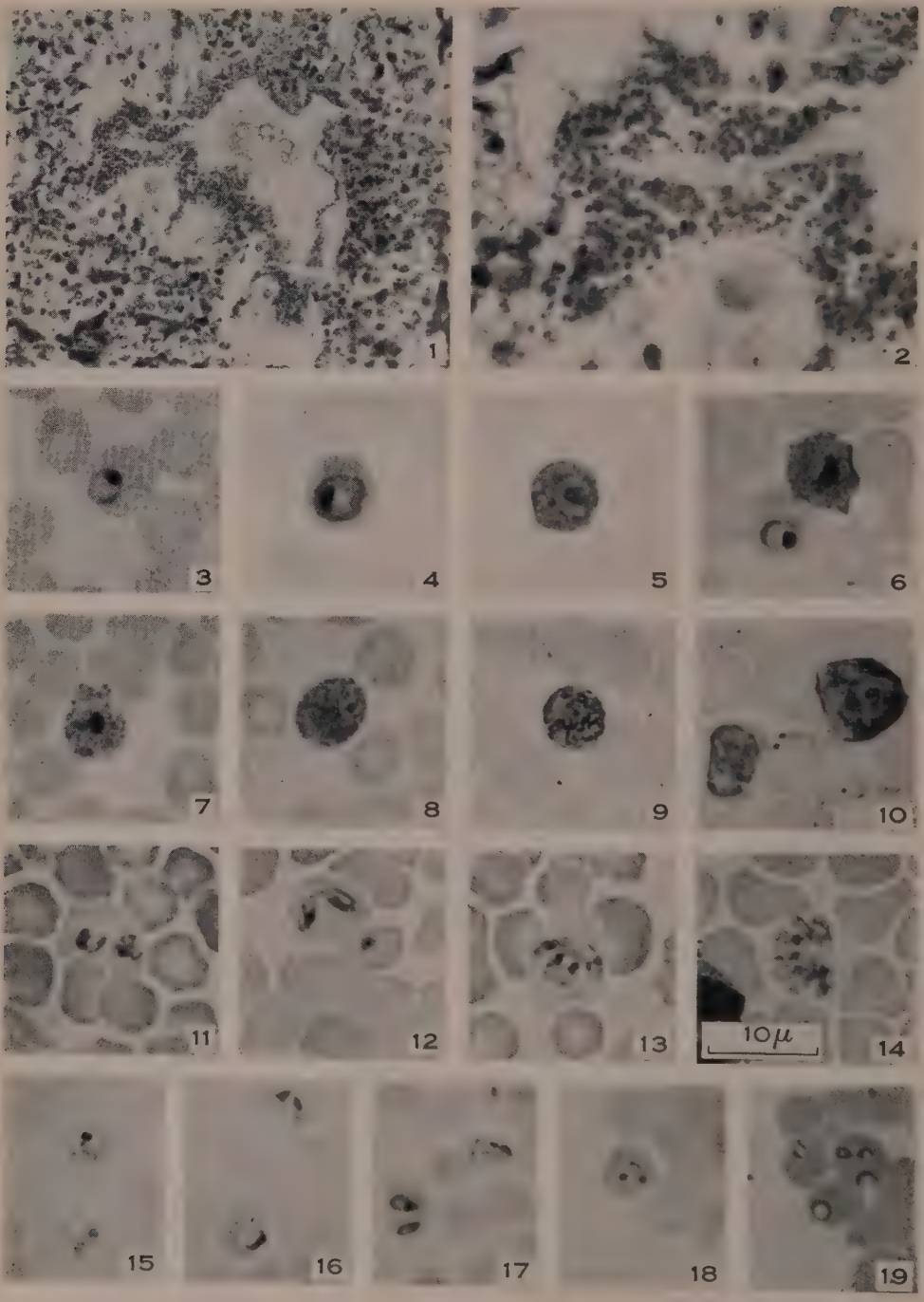

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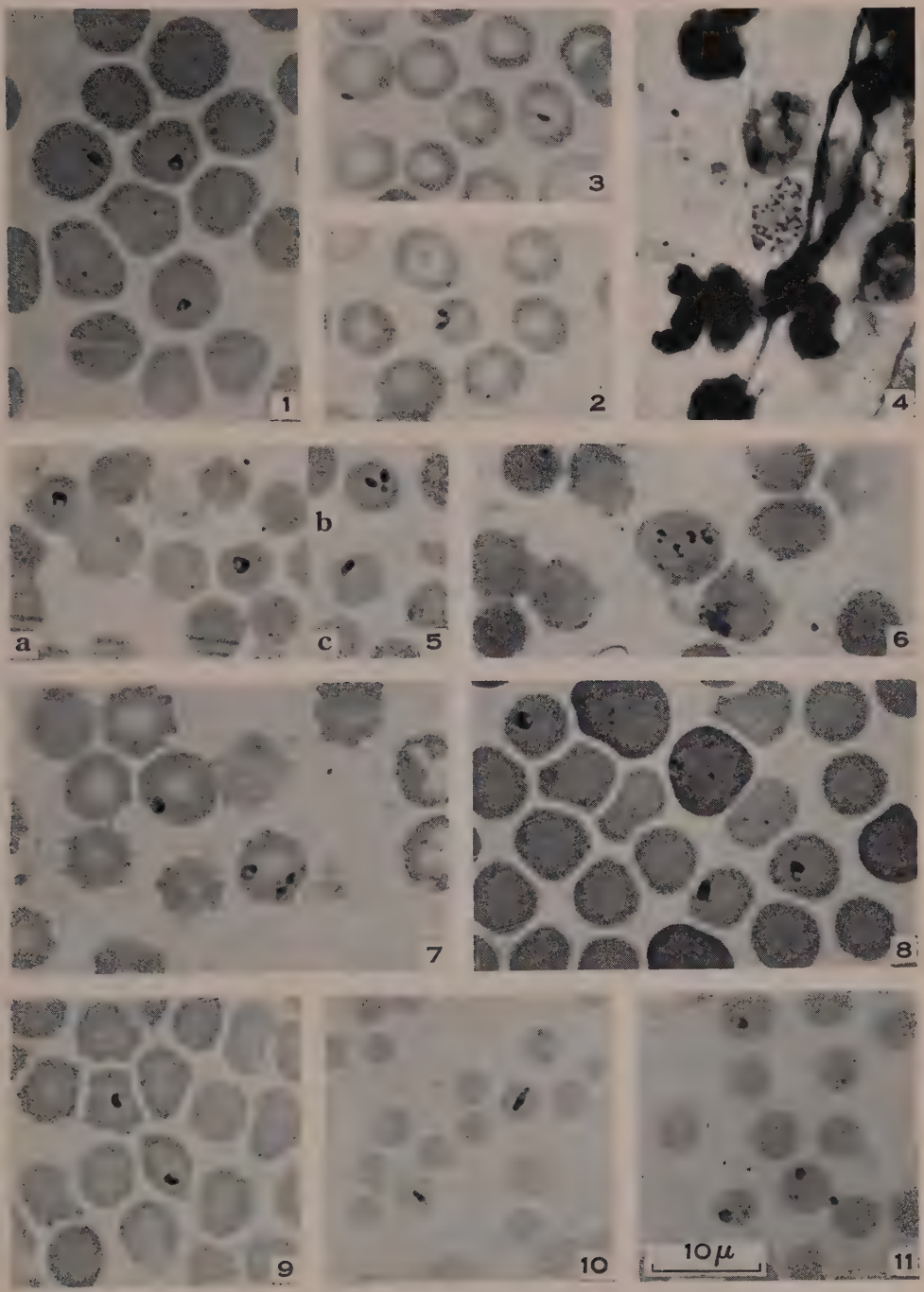

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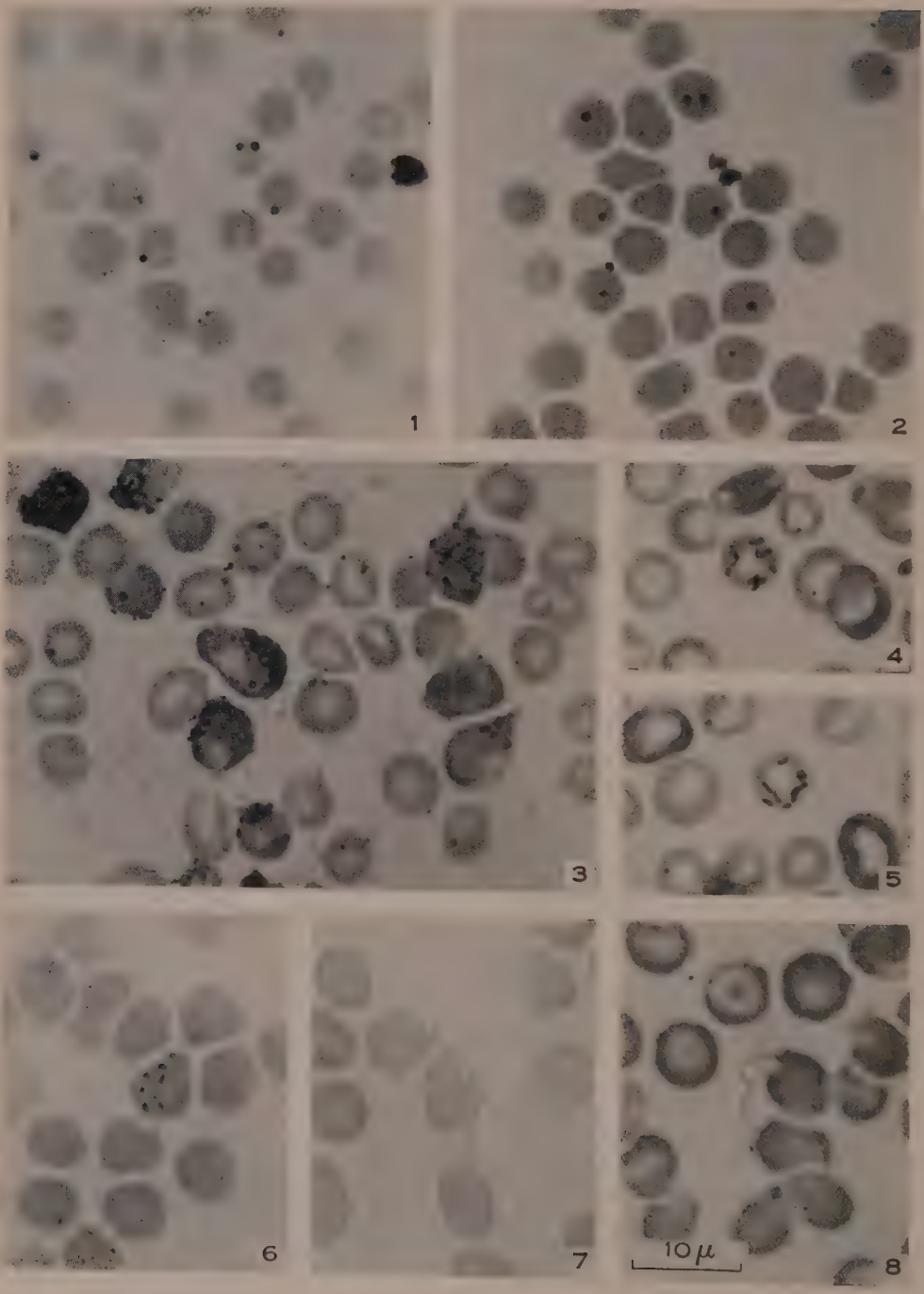


Plate 4

Figures 1 and 2 are photomicrographs taken by Mr. S. Woodward Smith, University of Sydney, and reproduced by courtesy of Mr. J. J. Lawrence, School of Public Health and Tropical Medicine, Sydney. Figures 3–19 were taken at the same magnification

Fig. 1.—Section of liver of *Pteropus scapulatus* showing merocyst of *Hepatocystis pteropi*. ×300.

Fig. 2.—Enlarged portion of merocyst. ×1000.

Figs. 3–6.—*H. pteropi* in the blood of *Pteropus conspicillatus*: 3, young ring; 4, large ring; 5, male gametocyte; 6, female gametocyte and ring.

Figs. 7–10.—*Polychromophilus melanipherus* in the blood of small bats: 7, female gametocyte from *Miniopterus blepotis*; 8, male gametocyte from *Vespadelus pumilis*; 9, female gametocyte from *Nyctophilus bifax*; 10, female gametocyte and immature form from *Hipposideros semoni*.

Figs. 11–14.—*Babesia thylacis* in the blood of *Thylacis obesulus*.

Figs. 15–17.—*B. bigemina* in the blood of cattle.

Figs. 18 and 19.—*B. argentina* in the blood of cattle.

Plate 5

Figs. 1–3.—*Theileria tachyglossi* in the blood of *Tachyglossus aculeatus*.

Fig. 4.—Presumed schizont of *Th. tachyglossi* in spleen smear of *T. aculeatus*.

Figs. 5.—*a*, *b*, and *c*: *Th. ornithorhynchi* in the blood of *Ornithorhynchus anatinus* from Upper Brookfield, S. Qld.

Fig. 6.—*Th. ornithorhynchi* in the blood of *O. anatinus* from Innisfail, N. Qld.

Figs. 7 and 8.—*Th. peramelis* in the blood of *Thylacis obesulus*.

Fig. 9.—*Th. peramelis* in the blood of *Potorous tridactylus*.

Figs. 10 and 11.—*Th. mutans* in the blood of cattle.

Plate 6

Fig. 1.—*Anaplasma marginale* in the blood of a calf.

Fig. 2.—*A. centrale* in the blood of a cow.

Fig. 3.—*Eperythrozoon coccoides* in the blood of *Mus musculus*.

Figs. 4 and 5.—*Haemobartonella muris* in the blood of *Rattus norvegicus*.

Fig. 6.—? *Haemobartonella* sp. in the blood of *Thylacis obesulus*.

Fig. 7.—*Borrelia* sp. in the blood of *T. obesulus*.

Fig. 8.—*Borrelia* sp. in the blood of *Macropus major*.

A REVISION OF THE GENUS *APHILEUS* CANDÈZE (COLEOPTERA: ELATERIDAE)

By A. Neboiss*

[*Manuscript received December* 12, 1958]

Summary

The genus *Aphileus* Candèze is restricted to the Australian mainland. It includes five species of which three—*A. distinctus*, *A. mulkanus*, and *A. goombarus*—are described as new. The synonymy of *A. lucanoides* Candèze and *A. depressus* Candèze as given by Schwarz (1907) and Schenkling (1927) is found to be correct.

Introduction

This paper deals with the systematics of the genus *Aphileus* Candèze, which is closely related to the genus *Hapatesus* Candèze. All species belonging to this genus are of medium to large size, somewhat flattened, with protruding mandibles, and are somewhat reminiscent of a lucanid in appearance.

Label data on specimens indicate that the main area of distribution lies on the eastern part of the continent (Fig. 1). According to Wood (1949) the localities are associated with savannah woodland, dry and wet sclerophyll forest, and rain-forest. The only exception is a single specimen (in the Australian Museum) of *A. lucanoides* from Tammin, W.A., which is thus associated with dry sandy heath country.

There are no publications either on the biology or ecology of any of the species in this genus, but Mr. F. E. Wilson stated (in litt.) that his specimens of *A. lucanoides* from Cascade, N.S.W., were taken under rotted native pine logs. In the National Museum collection there is a cast larval skin labelled by H. J. Carter "Larva case of *Aphilus* (sic) *lucanoides* hatched after 18 months in bottle. 18.12.04. H.J.C." As no adult specimen is associated with this skin, nor locality given, its identity cannot be confirmed. Figures 13 and 14 show dorsal views of the head capsule and 9th abdominal segment respectively of this cast skin.

The majority of specimens (where data are available) have been collected in December or January, but a few were taken in March.

Detailed locality and collection data are given for new species only. The collections from which specimens were examined are listed hereunder, together with abbreviations used in the text.

AM	Australian Museum, Sydney.
AS	Private collection of Mr. A. Smith, Melbourne.
BM	British Museum (Natural History), London.
CD	Private collection of Mr. C. Deane, Caloundra, Qld.
DEI	Deutsches Entomologisches Institut, Berlin.
ETS	Private collection of Mr. E. T. Smith, Melbourne.
FEW	Private collection of Mr. F. E. Wilson, Melbourne.
FTF	Private collection of Mr. F. T. Fricke, Sydney.

*National Museum of Victoria, Melbourne.

HSPA	Hawaiian Sugar Planters Association, Honolulu.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels.
NM	National Museum of Victoria, Melbourne.
NRS	Naturhistoriska Riksmuseet, Stockholm.
QM	Queensland Museum, Brisbane.
QU	Queensland University, Brisbane.
SAM	South Australian Museum, Adelaide.
WADA	Western Australian Department of Agriculture, Perth.
ZM	Zoologisches Museum, Humboldt University, Berlin.

Genus APHILEUS Candèze

Aphileus Candèze 1857, Mem. Soc. Sci. Liege **12**: 185.

Type species *Aphileus lucanoides* Candèze, 1857.

Medium to large, black or brownish black species, rather solidly built, easily distinguished by their protruding mandibles from all other genera in the subfamily Ctenicerinae.

Fig. 1.—Map showing distribution of species of the genus *Aphileus*.

Head moderately large to large, frontal carina incomplete, wider than long with an anterior central depression. Labrum large, semicircular, semi-elliptic, or almost rectangular. Mandibles large, protruding, bidentate or tridentate, almost horizontal. Maxillary palps with terminal segment hatchet-shaped. Antennae short; 1st segment long, slightly bent, and thickened at the apex; 2nd segment very short, 3rd usually at least twice as long as 2nd; succeeding ones somewhat flattened, shorter than 3rd; segments 4–10 diminishing in length, 11th about as long as 4th, oval, recessed on either side near the apex.

Pronotum wider than long, flattened, more or less densely punctate, anterior margin recessed to accommodate the head, sides curved, posterior angles strongly

diverging, carina very short. Prosternum short and wide, sutures fine, diverging anteriorly; mucro bent upward behind the fore coxae.

Scutellum shield-like, sides more or less parallel, central part somewhat depressed. Elytra wide and oval, rounded or flattened, lateral margins recurved; striae narrow, formed by single rows of punctures; intervals wide, flat or slightly convex.

Tarsi simple, segments 1–4 diminishing in length, 5th about as long as 3rd and 4th together, densely pilose beneath.

Key to Species of the Genus Aphileus

1. Prosternum punctate 2
   Prosternum verrucate ..... *A. lucanoides* Cand.
2(1). Head about half the length of pronotum, labrum semicircular or semi-elliptic 3
   Head nearly as long as pronotum, labrum almost rectangular ..... *A. ferox* Blackb.
3(2). Anterior legs with 1st tarsal segment shorter than 5th 4
   Anterior legs with 1st tarsal segment longer than 5th ..... *A. goombarus*, sp. nov.
4(3). Pronotum moderately punctate, interspaces shiny ..... *A. mulkanus*, sp. nov.
   Pronotum densely punctate, interspaces with waxy lustre ..... *A. distinctus*, sp. nov.

Aphileus distinctus, sp. nov.

Figs. 2–4; Plate 1, Fig. 1

Brownish black to black species with waxy lustre, 21–27 mm in length excluding mandibles, which are 3–4 mm in length. Head about as long as wide, densely punctate, central anterior part slightly depressed. Antennae short, dark brown, 1st segment as long as 2nd and 3rd together. Labrum semi-elliptic. Mandibles of male slender, as long as the head, acute at apex, with a small tooth on the dorsal ridge about one-third from apex, and another larger tooth on the inner margin about two-thirds from apex. Mandibles of female shorter and stouter, with short tooth on the inner margin about one-third from apex, dorsal tooth absent.

Pronotum wider than long, widest at its anterior third, densely punctate, covered with short yellowish white or whitish semidecumbent pubescence; posterior angles short, diverging; carina short and parallel to the lateral margin.

Scutellum slightly longer than wide, anterior margin straight, margins elevated and darker in colour. Elytra evenly rounded, widest at the posterior third, lateral margins flat and recurved; striae narrow, sharply defined, and formed by elongate parallel-sided punctures; intervals wide, flat, and indistinctly wrinkled as well as finely and sparsely punctate; covered with pale yellowish semidecumbent pubescence.

Legs dark brown; tarsal segments 1–4 of the anterior legs very short; 5th about as long as or slightly longer than 1st and 2nd together.

Prosternum moderately punctate, anterior margin rounded; prosternal grooves slightly curved, diverging anteriorly; mucro straight, bent upward behind the fore coxae.

Aedeagus as in Figure 2; hairs along the posterior edge of 8th sternite in the male are somewhat lanceolate at the apical third (Fig. 3(*a*)).

Lamina dentata (Fig. 4) short, strongly toothed along one lateral margin.

Type material.—Holotype ♂: "Kuranda, N. Qld., Jan. 1905, F. P. Dodd" (NM); allotype ♀: "Mutchilba, N. Qld., Mar. 1933, A. D. Selby" (FEW); paratypes: 1♂, "Cape York, N. Qld., C. French Coll." (NM); 1♂, "N.W.A." (presumably north-western Australia) (SAM).

Specimens examined.—Types plus 1♂ "N.W.A." (QU) which differs in the shape of its pronotum and was therefore not selected as paratype.

Distribution.—Northern Queensland and north-western Australia.

The form of pronotum and mandibles separates this species from others in this genus.

Aphileus lucanoides Candèze

Figs. 5–14; Plate 1, Fig. 2

Aphileus lucanoides Candèze, 1857, Mem. Soc. Sci. Liege **12**: 184, pl. 3, fig. 5.
Aphileus depressus Candèze, 1857, Mem. Soc. Sci. Liege **12**: 185.
Dorcastoma (*Elater*) *jansoni* Newman, 1857, Trans. Ent. Soc. Lond. (N.S.) **4**: 52.
Aphileus lucanoides Gumminger and Harold, 1869, Cat. Col. **5**: 1496.
Aphileus lucanoides Schwarz, 1907, Gen. Ins. **46**: 231.
Aphileus lucanoides Schenkling, 1927, Col. Cat. **11**(88): 406.
Aphileus lucanoides var. *depressus* Elston, 1930, Ark. Zool. **22**: 18.
Aphileus depressus Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.
Aphileus lucanoides Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.

Although Candèze believed that *lucanoides* and *depressus* could only be varieties of the same species he still described them as two separate species with the following remark:

"Je ne puis m'assurer si cette opinion est fondée et conséquemment s'il convient de les réunir ou de les séparer; dans le doute, je les décris sous des noms différents".

Some catalogues (Schwarz 1907; Schenkling 1927) have listed *depressus* in the synonymy of *lucanoides*, but without stating the reason for this decision.

Three specimens in the IRSNB collection bear red "type" labels, whereas the original description was based on a single specimen from the Deyrolle Collection, indicated by Candèze, with doubt, as coming from the East Indies. He included the following note:

"Je l'ai reçu de M. Deyrolle, sans nom, confondu avec des Lacon et indiqué avec doute comme venant des Indes Orientales. Je le crois du même pays que l'espèce qui suit".

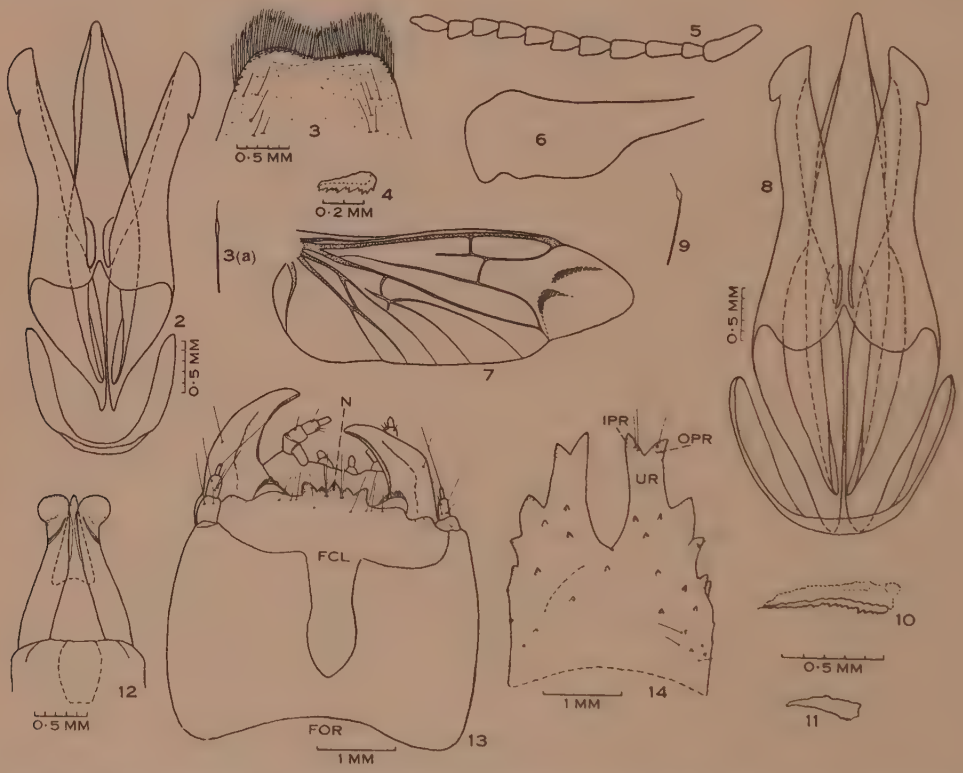
Not one of the three specimens bears a corresponding label and consequently cannot include the type.

As the Deyrolle Collection finally went to the British Museum via Janson's Collection it seems safe to assume that types described by Candèze from Deyrolle material are therefore now in the BM collection. A specimen discovered in the latter collection has attached identification labels, one reading "*Aphileus lucanoides*" in Candèze's handwriting, a second with the printed number "266", and a third reading "Janson coll. 1903–130". This specimen fully agrees with Candèze's description, and is now selected as the lectotype of *lucanoides*.

The original description of *depressus* is based on two specimens, one from the Deyrolle, the other from the Chevrolat Collection. Deyrolle's specimen, which is in the BM collection is labelled with four labels: "*Aphileus depressus*" in Candèze's

handwriting, "M. Bay" (Moreton Bay?), "267", and "Janson coll. 1903 -130", is now selected as the lectotype of *depressus*. The Chevrolat Collection went to the Paris Museum via the Fleutiaux Collection, and probably Chevrolat's specimen of *depressus* is now in that museum.

Both lectotypes selected above are females and, apart from their differences in colour and shape of pronotum and elytra, other important characters including the lamina dentata and the transversely verrucate prosternum are identical, supporting the previously proposed synonymy of *lucanoides* and *depressus*.



Figs. 2–4.—*A. distinctus*, sp. nov.: 2, aedeagus (holotype); 3, posterior edge of 8th sternite of the male; 3*a*, hair from the posterior edge of 8th sternite of the male; 4, lamina dentata (allotype). Figs. 5–14.—*A. lucanoides* Cand.: 5, antenna; 6, portion of posterior coxa; 7, wing venation; 8, aedeagus; 9, hair from the posterior edge of 8th sternite of the male; 10, lamina dentata (lectotype); 11, lamina dentata from a small-sized female; 12, female external genitalia; 13, larval head, dorsal view; *FCL*, frontoclypeal region; *FOR*, foramen magnum; *N*, nasale; 14, 9th abdominal segment of larva, dorsal view; *IPR*, inner prongs; *OPR*, outer prongs; *UR*, urogompi.

The synonymy of *Dorcastoma jansoni* appears to be correct, as the description of this latter species agrees well with specimens of *lucanoides*. The type location of *D. jansoni* is not known to the author.

Examination of a large number of *lucanoides* specimens has shown great variability in size, shape of pronotum and elytra, and colour. While males were

generally found to be smaller, variability in colour was not found to be consistently associated either with sex or with geographical distribution.

Dark brown or brownish black species, 17–33 mm in length (excluding the mandibles which are 1·5–2·5 mm in length), strong, stout, acute at apex, with a strong pointed tooth on the inner margin about half way from the apex. Head flat or slightly depressed in the middle.

Pronotum dull brownish black, sparsely punctate with fine shallow punctures, covered with yellowish brown semidecumbent hairs; lateral margins semicircular, posterior angles diverging, carina short.

Elytra with a waxy lustre, moderately covered with yellowish semidecumbent hairs, broad, somewhat depressed; lateral margins widened and flattened; striae shallow, formed from elongate punctures, intervals flat or slightly convex, sparsely and minutely punctate.

Legs dark brown, tarsi simple, pilose beneath, posterior coxae narrow on the outside, but abruptly widened towards the middle.

Ventral surface covered with short stout decumbent hairs. Prosternum transversely verrucate, in smaller specimens less distinctly so than in larger ones; sides almost straight, gradually diverging anteriorly.

Aedeagus as in Figure 8; hairs along the posterior edge of 8th sternite in the male are spatulate near the apex (Fig. 9).

Lamina dentata (Figs. 10 and 11) short, strongly toothed at the base. Figure 10 drawn from the type specimen (BM); Figure 11 from a very small specimen in the SAM.

A brief description of larval characters is given from the above-mentioned larval skin. The terminology used in this paper is that of Glen (1950):

Larva (Figs. 13, 14) unicolorous yellowish brown, head capsule dark yellowish brown, mandibles black distally. Length of the cast skin 26 mm. Nasale 5-pointed; frontoclypeal region pointed posteriorly, not extending backward to foramen magnum. Urogompi with inner prongs and outer prongs almost equal in length. Dorsum of 9th abdominal segment covered with sharp teeth, setae damaged and their position uncertain.

Type locality.—"Australia".

Type location.—lucanoides: BM; *depressus*: BM (see discussion above).

Specimens examined.—142 (AM; AS; BM; CD; DEI; ETS; FEW; FTF; HSPA; IRSNB; NM; NRS; QU; SAM; ZM).

Distribution.—QUEENSLAND: Cairns, Atherton, Malanda, Herberton, Kuranda, Inkerman (near Townsville), Chillagoe, Ravenshoe, Millaa Millaa, Ayr, Brisbane, National Park (Macpherson Range), Bunya Mts., Wide Bay, Killarney, Mt. Tamborine, Moreton Bay. NEW SOUTH WALES: Richmond R., Dorrigo, Mullumbimby, Ebor, Cascade, Illawarra, Murrurundi. WESTERN AUSTRALIA: Tammin.

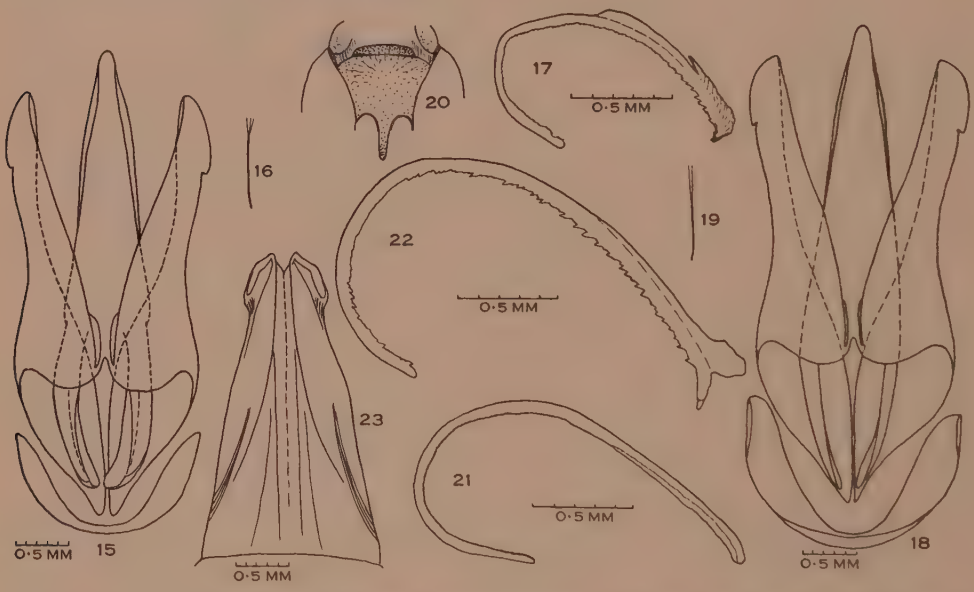
APHILEUS MULKANUS, sp. nov.

Figs. 15–17; Plate 1, Fig. 3

Reddish black to black shiny species, 25–29 mm in length, mandibles protruding another 2 mm. Head about as wide as or only a fraction wider than long, almost

rectangular, moderately punctate, anterior median portion depressed, anterolateral angles at the base of antennae not excessively elevated, but more pronounced than in *lucanoides*. Antennae dark reddish brown, short, 1st segment about as long as 2nd and 3rd together. Labrum semicircular. Mandibles strong, acute at the apex, a stout, pointed, sometimes bicuspidate tooth on the inner margin, males with an additional small tooth on the dorsal ridge, both about one-third to half way from the apex.

Pronotum evenly rounded, moderately punctate, interspaces shiny, covered with fine yellowish semidecumbent hairs; posterior angles short, diverging; carina short and parallel to the lateral margin.



Figs. 15–17.—*A. mulkanus*, sp. nov.: 15, aedeagus (allotype); 16, hair from the posterior edge of 8th sternite of the male; 17, lamina dentata (holotype). Figs. 18–21. *A. ferox* Blackb.: 18, aedeagus; 19, hair from the posterior edge of 8th sternite of the male; 20, prosternum (male); 21, lamina dentata (type). Figs. 22, 23.—*A. goombarus*, sp. nov.: 22, lamina dentata (holotype); 23, female external genitalia.

Elytra evenly rounded, widest at the posterior third, sparsely covered with fine yellowish semidecumbent hairs, lateral margins recurved; striae rather shallow, formed by elongate punctures; intervals indistinctly wrinkled, finely and sparsely punctate.

Anterior tarsi with 5th segment as long as or longer than 1st and 2nd together.

Prosternum rather coarsely punctate, slightly wrinkled along the anterior margin; mucro slightly bent upward behind the fore coxae; prosternal sutures bent and diverging anteriorly.

Aedeagus as in Figure 15; hairs along the posterior edge of the 8th sternite split at the apex (Fig. 16).

Lamina dentata (Fig. 17) similar to that of *A. goombarus*, but differing in its smaller size and in the arrangement of spines.

Type locality.—Jandowae, Qld.

Specimens examined.—Holotype ♀, "Jandowae, Qld. R. Illidge" (QM); allotype ♂, "Bulimba, Qld. 24.xii.1908" (QM) (both specimens presented by QU); 1 ♀ paratype, "Jandowae, Qld. R. Illidge" (QU); 3 ♀♀ paratypes, "Carnarvon Rge. Qld. 16.i.1940. N. Geary" (AM; NM, 1 ♀ presented by AM); 1 ♀ paratype, "Cairns" (SAM); plus 2 ♂♂ without locality data, distinctly smaller (BM), and not selected as paratypes.

Distribution.—Queensland.

The name is derived from an aboriginal name meaning "dark", used by the natives of the Condamine R. district, Qld.

Aphileus ferox, Blackburn

Figs. 18–21; Plate 1, Fig. 4

Aphileus ferox Blackburn, 1895, Trans. Roy. Soc. S. Aust. **19**: 50.
Aphileus ferox Schenkling, 1927, Col. Cat. **11**(88): 406.
Aphileus ferox Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.

Reddish black to black shiny species, 31–33 mm in length excluding the mandibles. The latter are approximately 5 mm in length, protruding horizontally forward, pointed at the apex, and each bearing a strong pointed tooth on the inner margin about two-thirds from the apex, and a very small tooth on dorsal ridge about one-third from the apex. Labrum almost rectangular, anterior margin straight. Head very large, a fraction wider than long, somewhat depressed at the anterior central part, coarsely punctate, sparsely covered with fine yellowish semidecumbent hairs, anterolateral angles at the base of antennae distinctly elevated. Antennae short, 1st segment as long as 2nd and 3rd together.

Pronotum more than 1·5 times wider than long, depressed, moderately to coarsely punctate, covered with fine yellowish semidecumbent hairs; anterolateral angles produced forward, barely reaching the posterior margin of eyes; sides rounded, posterior angles short, diverging; carina short and deviating from lateral margin.

Scutellum slightly longer than wide, flat, with faintly elevated median line and elevated median sections of anterior and lateral margins; minutely and sparsely punctate. Elytra slightly depressed, widest at the posterior third; striae narrow, sharply defined, formed by elongate punctures; intervals flat or slightly convex, indistinctly wrinkled, finely and sparsely punctate, covered with yellowish semidecumbent hairs; suture ending with a short triangular spine.

Prosternum short and wide, anterolateral angles recessed (Fig. 20), unevenly and moderately punctate, more densely so along the anterior margin where also indistinct radial wrinkles are present. Mucro bent upward behind the anterior coxae, apex slightly recurved.

Aedeagus (Fig. 18) drawn from a specimen in NM collection; hairs along the posterior edge of 8th sternite split at the apex (Fig. 19).

Lamina dentata (Fig. 21) with a row of very fine teeth.

Type locality.—North Queensland.

Type location.—BM.

Specimens examined.—1 ♂, "Cape York" (NM). Miss C. von Hayek very kindly examined the type ♀ in the BM collection and supplied the required information.

Distribution.—North Queensland.

Aphileus goombarus, sp. nov.

Figs. 22, 23; Plate 1, Fig. 5

♀. Brownish black to black species, 40 mm in length excluding mandibles. The latter are 3·5 mm in length, stout, blunt at the apex, with a strong tooth on the inner margin near the middle. Labrum semi-elliptic. Head wider than long, dull black, moderately punctate, anteromedian part depressed, anterolateral angles at the base of antennae elevated. Antennae short, 1st segment almost as long as 2nd, 3rd, and 4th together.

Pronotum wider than long, moderately punctate, more densely so along the sides, moderately covered with short yellowish semidecumbent hairs, lateral margins rounded, anterolateral angles produced forward, reaching the median line of the eyes; posterior angles short, carinate, and strongly diverging.

Scutellum shield-like, slightly wider than long, widest at the posterior third, posterior margin flatly rounded. Elytra brownish black to black with waxy lustre, widest at the posterior third, rounded at the apex; suture ending with a short spine; lateral margins flat and recurved; striae fine, formed by elongate punctures; intervals flat or slightly convex, indistinctly wrinkled, sparsely and minutely punctate, moderately covered with short yellowish semidecumbent hairs.

Legs dark brown, anterior pair with 1st tarsal segment longer than 5th.

Prosternum moderately punctate, anterior margin evenly rounded, prosternal sutures fine, almost straight, diverging anteriorly; mucro bent upward behind the fore coxae, apex recurved.

Lamina dentata (Fig. 22) with widened and notched basal end.

♂. Unknown.

Type locality.—Lake Grace, W.A.

Type location.—NM (presented by WADA).

The form of mandibles distinguishes this species from *A. ferox*; the more pointed elytra and shape of pronotum from *A. mulkanus*.

The name is derived from an aboriginal name meaning "big" used by aborigines of the Kojonup district, W.A.

Acknowledgments

The author is greatly indebted to the Institutions and private collectors listed in the Introduction for the loan of specimens. Especial thanks are due to Miss Christine von Hayek, British Museum (Natural History), London; Dr. J. M. Vrydagh, Institut Royal des Sciences Naturelles de Belgique, Brussels; Dr. J. W. Evans, Australian Museum, Sydney; and Mr. C. F. H. Jenkins, Western Australian Department of Agriculture, Perth.

REVISION OF THE GENUS APHILEUS

10 MM

References

Glen, R. (1950).—*Smithson. Misc. Coll.* **111**(11): 1–246.

Schenkling, S. (1927).—"Coleopterorum Catalogus". Vol. 11. Pt. 88. p. 406. (Ed. W. Junk.) (The Hague.)

Schwarz, O. (1907).—"Genera Insectorum". Vol. 46. p. 231.

Wood, J. G. (1949).—Vegetation map of Australia. In "The Australian Environment". pp. 88, 89. (C.S.I.R.O.: Melbourne.)

Explanation of Plate 1

Photographs by the author

Fig. 1.—*A. distinctus*, sp. nov., ♂, holotype, Kuranda, Qld.

Fig. 2.—*A lucanoides* Cand., ♀, Queensland (specimen from IRSNB).

Fig. 3.—*A. mulkanus*, sp. nov., ♀, holotype, Jandowae, Qld.

Fig. 4.—*A. ferox* Blackb., ♂, Cape York, Qld. (specimen from NM).

Fig. 5.—*A. goombarus*, sp. nov., ♀, holotype, Lake Grace, W.A.

A REVISION OF THE GENUS *TYROPHAGUS*, WITH A DISCUSSION ON ITS TAXONOMIC POSITION IN THE ACARINA

By Phyllis L. Robertson*

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Summary

Tyrophagus is considered as a world-wide genus. Its complex history is traced and its position in the Acarina is re-examined against the background of recent classification changes.

Eleven species of *Tyrophagus* are recognized and keyed.

Neotypes are designated and described for *putrescentiae* Schrank, 1781, and *longior* Gervais, 1844, and a case is made for declaring *dimidiatus* Hermann, 1804, a species name brought into the group by A. C. Oudemans, to be a *nomen dubium*.

Lectotypes are indicated for *australasiae* Oudemans, 1916, *javensis* Oudemans, 1916, *vanheurni* Oudemans, 1924, *deliensis* Oudemans, 1923, and *muris* Oudemans, 1924. Of these, the last two are treated as uncertain species, while *vanheurni* is judged to have no status.

T. palmarum Oudemans, 1924, and *T. perniciosus* Zakhvatkin, 1941, are redescribed, and three species are described as new.

Introduction

Members of the genus *Tyrophagus* were probably amongst the earliest free-living mites recognized as pests (Oudemans 1929), and one or more economic species has been recorded from every continent—from Canada (Jarvis 1906; Nesbitt 1945), United States of America (Osborn 1893; Banks 1906; Baker and Wharton 1952), South America (Mayer and Hack 1953), from Europe (Oudemans 1924*a*, 1924*b*, 1926; Vitzthum 1929), Africa (Willcocks 1925; Ghesquiere 1947), Asia (Vitzthum 1926), Australia (Rainbow 1906; Womersley 1941)—and from many islands, such as those of the West Indies (Banks 1917), Ceylon (Hirst 1912), Java, Sumatra, Amboina, New Guinea (Oudemans 1916, 1923, 1925), Japan (Sasaki 1927), Formosa (Sugimoto 1938, 1940), and New Zealand (Cockayne and Waters 1916; Robertson 1946). Recent discussions (Zakhvatkin 1941; Solomon 1943; Baker and Wharton 1952) on the many fields in which annoyance is caused and damage inflicted by mites of the superfamily Acaroidea (formerly called Tyroglyphoidea) contain numerous references to representatives of the genus. They are serious laboratory pests of insect and fungus cultures (Jewson and Tattersfield 1922; Page and Shafik 1936; Norris 1946). They are important in the field of medicine (Lapage 1945) as a cause of dermatitis (Castellani 1912; Hirst 1920; Dowling and Thomas 1942), of conjunctivitis (Findlay 1921), of intestinal acariasis (Hinman and Kampmeier 1934), and of bronchial asthma (Carter and D'Abrera 1946). In veterinary science, they are recognized as contaminating fodder such as hay, thereby producing

* School of Public Health and Tropical Medicine, University of Sydney.

intestinal disorders in horses, dogs, and other animals (Zimmerman 1918; Newstead and Morris 1920; Solomon 1943). In agriculture, species of *Tyrophagus* interfere with the cultivation of mushrooms (Jary and Stapley 1937; Davis 1944) and of various seedling plants (van den Bruel 1940; Baker and Wharton 1952), and may be responsible for heavy losses during the storage of tobacco (André 1933) and, most important of all, of grain and dairy products (Zakhvatkin 1941; Robertson 1946; Hughes 1948; Krantz 1955).

In consequence of the long history of *Tyrophagus*, its world-wide distribution, and the fact that much data on it has been published by economic entomologists working under conditions of isolation in which they have been unable to check their material with previously described specimens, nomenclature in the genus has reached a particularly serious state of confusion (compare, for example, Cotton and Good (U.S.A.) 1937; Nesbitt (Canada)1945; Bollaerts and Breny (Belgium) 1951).

Moreover, little type material of *Tyrophagus* remains in existence, and any which has been preserved is in poor condition. This has been due to technical difficulties involved in mounting members of the group, which were shrivelled and distorted by early mountants such as glycerine jelly and Canada balsam. It was probably not until the beginning of the present century or even later that gum chloral mountants, for example Berlese's fluid and other modifications of de Faure's earlier formula, provided, at least, a partial answer to the problem of preserving type slides. Since the rather numerous 19th century descriptions of species which may be assigned to *Tyrophagus* are unsupported by material preserved until the present day, later workers on the group have had the alternative of either selecting early names on the basis of personal preference (Oudemans 1924*b*; Hull 1931), or of ignoring early records and describing their species under current names (Hughes 1948).

Perhaps the most serious difficulty has been that of finding characters suitable for species separation. Throughout the genus there is remarkable uniformity in body size, colour, and hair development, just as there is in habitat preferences and behaviour, while the kind of morphological structures which may be capable of differentiation at species level are absent. This has led to the adoption of quantitative characters, such as leg segment measurements and body hair ratios, for species separation (Zakhvatkin 1941), but these are to some extent suspect on the grounds that they may be easily modified by environment.

The aim of the present review of *Tyrophagus* systematics, therefore, is to stabilize the names of common economic species, to find a means of compensating for the absence of type material, and to re-assess the characters used for species separation.

The work was undertaken in the first place as a background to an investigation of variation and speciation in populations of *Tyrophagus* infesting stored products (Robertson 1956). It is based on a series of mounts prepared for the variation study from fresh material collected by the author in New Zealand, the United Kingdom, the Netherlands, and Australia. The collection is mounted in Swan's (1936) modification of Berlese's fluid, and totals approximately 15,000 specimens on 1705 slides. In addition, examinations have been made of the 81

slides of *Tyrophagus* in the Oudemans Collection at the Rijksmuseum van Natuurlijke Historie, Leiden; a series of 44 slides of the type species from the U.S. National Museum, Washington; Vitzthum's material of *Tyrophagus* in the Zoologische Sammlung des Bayerischen Staates, Munich; and material, both mounted and preserved, in the School of Public Health and Tropical Medicine, Sydney, and the Royal College of Veterinary Science, Denmark, and from Canada, United States of America, Nigeria, Chile, and the Pacific island of New Britain.

The Taxonomic Position of Tyrophagus

According to Baker and Wharton (1952) *Tyrophagus* belongs to the suborder Sarcoptiformes, section Acaridiae, family Acaridae, and the subfamily Acarinae. Yunker (1955) follows the same general plan, regarding the Acaridiae as a supercohort, and introducing between that and the family Acaridae the cohort Acaridia and superfamily Acaroidea. Several of the names of these categories are comparatively recent, and it is of some interest to examine the complex situation lying behind the changes which have been made.

Nesbitt (1945) and Robertson (1946) traced the developments in classification of that section of the Acarina which includes *Tyrophagus* for the period from Michael (1901) to Zakhvatkin (1941). Michael's simple view of the relationships of the fourteen genera he recognized in what was then the family Tyroglyphidae followed directly from the earliest attempts to classify it by Koch in 1842, Mégnin in 1880, Canestrini (1888), Berlese (1897), and Canestrini and Kramer (1899). After Michael, in the early part of the present century, such workers as Banks, Oudemans, and Vitzthum described a multiplicity of new forms whose inclusion in the group at first greatly confused its classification. Zakhvatkin, however, was able to incorporate them in such a way as to form a natural group, the superfamily Tyroglyphoidea of the suborder Sarcoptiformes, and within it he placed *Tyrophagus* in the family Tyroglyphidae, subfamily Tyroglyphinae, and tribe Tyrophagini.

Recent Changes in Higher Categories

Between Zakhvatkin (1941) and Yunker (1955) several workers, including Hughes (1948) and Turk (1953), have divided the suborder Sarcoptiformes into supercohorts and cohorts, thus preserving Oudeman's conception of basic relationships in the group. It is nevertheless an unfortunate deviation from the accepted pattern of taxonomic classification, in that "cohort" is a category normally used between "class" and "order" (Mayr, Linsley, and Usinger 1953), not below "suborder" as in the present case. The arrangement is probably better eliminated, a step which can be achieved either:

(1) By maintaining the present status of the Acarina and Sarcoptiformes as order and suborder respectively, but subdividing the latter at superfamily level only—a course whereby the initial separation of the Acaridiae from the Oribatei would be lost; or

(2) By elevating the Acarina to a subclass, or possibly a superorder, and the Sarcoptiformes to an order, so that the Acaridiae and Oribatei would then become suborders.

Certainly to elevate the Acarina to a superorder, as suggested in (2) above, could scarcely unbalance any classification of the Arachnida which might be accepted within the near future. But having regard for the complexity and present-day importance of the Acarina as a group, it would appear that any change made should be a more real and definite one. The view that the Acarina should be given the status of a subclass of the Arachnida, as implied by André (1949) and suggested by Baker and Wharton (1952), is therefore accepted here as the most satisfactory one. The change has been incorporated in the present work, in which also the Sarcoptiformes are treated as an order and the Acaridiae as a suborder.

Superfamily, Family, and Subfamily Name Changes

Zakhvatkin's terminology for these categories was based on the name *Tyroglyphus*, which was long accepted as the genus of the grain mite, *Acarus siro* L., formerly *Tyroglyphus farinae*. According to Oudemans (1897) *Tyroglyphus* and its nearest allies, of which *Tyrophagus* is one, were first separated from other Acaridiae in 1868 by Donnadieu under the name "Tyroglyphiens". Since then members of the group have become known by the familiar name "tyroglyphids", and the family Tyroglyphidae has continued to be used up to the present, perhaps most recently by Radford (1950) and Hughes (1957).

But the case put forward by Ewing and Nesbitt in 1942 for changing the generic name *Tyroglyphus* to *Acarus* foreshadowed possible alterations in family-group names based on *Tyroglyphus*. About the same time Green and China (1943), supported by the Committee on Generic Nomenclature of the Royal Entomological Society of London, expressed the opinion that a change of family name was not always justified on the basis of a name change in the type genus, such as had been proposed in the present case. Later again the International Commission on Zoological Nomenclature, in their Copenhagen Decisions (Hemming (Ed.) 1953), made a ruling that family-group names should no longer be subject to alteration solely on these grounds, but should be governed by priority.

However, Ewing and Nesbitt (1942) pointed out that *Tyroglyphus* is not an available synonym of *Acarus* but an absolute synonym, and this has recently been confirmed by Declaration No. 94 of the International Commission on Zoological Nomenclature, which has placed *Tyroglyphus* on its "Official Index of Rejected and Invalid Generic Names in Zoology". Thus, although as a group Tyroglyphidae has priority over Acaridae, and despite the familiar use of "tyroglyphids" for members of the group, at the present time the family name Tyroglyphidae appears to be ruled out completely by the invalidity of the generic name on which it is based.

Since Donnadieu's name Tyroglyphidae cannot be recognized, it appears from Oudemans (1897) that the name Acarini used by Canestrini and Fanzago in 1877 assumes priority, so that it would be more correct to attribute the family Acaridae to the latter two authors than to continue the present-day practice of attributing it to Nesbitt (1945).

Although Zakhvatkin's (1941) inclusion of the Acaridae, Saproglyphidae, and Glycyphagidae in the Tyroglyphoidea is generally accepted as the first attempt to

group these families into a superfamily, since the root of his superfamily name is invalid it must be replaced by the Acaroidea of Yunker, 1955.

It is accepted here that the minor group based on the genus *Acarus* is sufficiently distinct to warrant continuation of its status as a subfamily, the Acarinae, but *Tyrophagus* and some allied genera were separated from it by Oudemans (1924*a*), and the separation should be recognized in naming the group in which *Tyrophagus* is placed. The increased importance of the *Tyrophagus* group in relation to the Acaridae as a whole, which systematic studies of the past twenty years have demonstrated, justifies its being treated also as a subfamily.

Thus, according to the views held herein, the genus *Tyrophagus* falls within the

Subclass Acarina Nitzsch, 1818
Order Sarcoptiformes Reuter, 1909
Suborder Acaridiae Latreille, 1802
Superfamily Acaroidea Yunker, 1955
Family Acaridae Canestrini & Fanzago, 1877
Subfamily Tyrophaginae Oudemans, 1924.

Historical Review

The Genus Tyrophagus

When Oudemans (1924*a*) first separated *Tyrophagus* from *Tyroglyphus*, *Tyrolichus*, and *Caloglyphus*, he regarded all four as subgenera of *Tyroglyphus* s.l., the genus which must now be dropped from the Acaroidea on the grounds of its invalidity (International Commission on Zoological Nomenclature, Hemming (Ed.) 1958).

The following is a translation of Oudemans' (1924*a*) description of *Tyrophagus*:

"*Tyrophagus* subgen. nov., type *Acarus putrescentiae* Schr. 1781. Diagnosis: inner hairs of the transverse row longer than outer; 'nuchaal' hairs marginal, far forward, beside the gnathosoma, long, hairy, medianly curved; hysterosoma with 3 pairs of short hairs (or brushes) including those in front of the oil glands; otherwise with long hairs. Hereunder also *dimidiatus* Herm., 1804 (syn. *longior* Gerv., 1844), *javensis* Oudms., 1916, *australasiae* Oudms., 1916, *deliensis* Oudms., 1920, *palmarum* Oudms., 1924. Of these hypopi are known."

Later in the same year Oudemans gave *Tyrophagus* full generic status, and again in the same year (1924*b*) he discussed the identity of its type species *putrescentiae*.

There is little doubt of Oudemans having been the first to recognize that the *Tyrophagus* species form a distinct and separate group, which his description defined adequately. Unfortunately he subsequently suggested that *Tyrophagus* was a synonym of the genus *Coelognathus* of von Hessling, 1852 (Oudemans 1937). This suggestion is being carried on by present-day authors, for example by Vitzthum (1940–43) who lists under *Tyrophagus* "(according to Oudemans = *Coelognathus* v. Hessling, 1852)", and by Baker and Wharton (1952), who state simply "(= *Coelognathus* v. Hessling, 1852)." It has culminated in the step taken by Turk (1953), who relegates *Tyrophagus* to synonymy and records *Coelognathus* as the

generic name. However, the generic name *Coelognathus* is not available for inclusion in the Acarina, as it was used in the Reptilia by Fitzinger in 1843 (see Neave 1939). This was discovered by Oudemans after his 1937 opinion was published and was later corrected (Oudemans 1938), but up to the present the correction has gone unnoticed.

The most serious problem threatening the taxonomic status of *Tyrophagus* concerns the identity of its type species. Zakhvatkin (1941) and other present-day acarologists have expressed the view that the *putrescentiae* of Schrank is unrecognizable, and have inferred that Oudemans' concept of this species was confused when he designated it the type of *Tyrophagus*. If these opinions are accepted, then *Tyrophagus* cannot continue to be recognized as a valid genus.

But it is obvious from his 1924*b* paper that Oudemans gave careful consideration to the identity of Schrank's *putrescentiae*. He recognized that Schrank's description contained little that was definitive, and that identification of the species must be based largely on its habitat. Accordingly he searched "under damp rotten leaves on damp humus", the habitat given by Schrank in 1776, and obtained his first specimens from there in 1902.

The accuracy with which Oudemans identified the species he called *putrescentiae* was checked by the present author while studying *Tyrophagus* material in the Oudemans Collection at the Rijksmuseum van Natuurlijke Historie, Leiden, in 1954. Twenty slides labelled *putrescentiae* are preserved, most of them carrying 20–30 mites per slide. These were collected during a period of 30 years, from 1902 to 1932, and five of them include some specimens different from the remainder. There can be little doubt, however, of the species which Oudemans recognized as *putrescentiae*, and all the 1924 material belongs to it.

Since Schrank's description conforms to the requirements of the International Rules of Zoological Nomenclature, and considering that Oudemans found his species in the same habitat, and that contrary to Zakhvatkin's opinion his collected material proves he had an adequate conception of its distinguishing characters, Oudemans' species is accepted here as being in fact the *putrescentiae* of Schrank, 1781. As it is agreed by acarologists that Schrank's material has been lost, it now becomes necessary to select a neotype (see p. 157) in order to place the identity of *putrescentiae* beyond question.

The Species of Tyrophagus

Oudemans' material of *Tyrophagus* was taken into account in reaching decisions on the names to be applied in the present work to common and widely distributed species of the genus. *Tyrophagus* is represented in the Oudemans Collection by 81 slides, containing several hundreds of specimens, which Buitendijk (1945) catalogues under 14 species. Oudemans' specimens were obtained from Holland, Germany, Belgium, Italy, etc., and also from tropical areas such as New Guinea, Java, Sumatra, and other Indonesian islands. He collected from natural habitats, and his *Tyrophagus* was found associated with living insects in ant and bee nests, beetle tunnels, etc., on dead insects, in the fur of animals, on seedling plants of rye and barley, on bulbs, fruits, nuts, seeds, in rotten plant material such as potatoes and palmstalks, and

even in brackish water. Several of the species more generally known as medical, veterinary, and agricultural pests were obtained from habitats such as these.

Some misidentifications were noted amongst Oudemans' slides of *Tyrophagus*. Where a series had been built up over a long period of time, errors were most likely to be found either near the beginning or the end of the series. In most cases, however, it was possible to select with reasonable certainty the material to which Oudemans intended his name should be applied. A list of all the slides of *Tyrophagus* in the Oudemans Collection forms an Appendix to the present author's thesis on the genus, which is in the University Library, Cambridge (Robertson 1956). This contains the species names Oudemans applied to his specimens, with a re-assessment of their identity in the light of current work and a record of misidentified slides.

Of the 14 species listed under *Tyrophagus* in the Oudemans Collection, 4 distinct species, 3 more which are probably distinct, and 3 doubtful ones can be recognized. The clearly separable species were named by Oudemans:

putrescentiae (Schrank, 1781) — *infestans* (Berlese, 1884)
dimidiatus (Hermann, 1804) — *palmarum* (Oudemans, 1924).

Of these, *putrescentiae* and *palmarum* are here accepted as valid names, but *dimidiatus* and *infestans* are not.

Great confusion has centred around the species which Oudemans called *dimidiatus*. Zakhvatkin (1941) does not recognize it amongst the species of *Tyrophagus* he describes and keys, while in the United Kingdom the name has been applied to at least three different species. For example, Hull (1931) used it for a stored-product form—one or other of the two species here called *palmarum* (p. 169) and *putrescentiae* (p. 157). Jary and Stapley (1937) adopted it for the field species now called *oudemansi* (pp. 154 and 167), and Hughes (1957) reintroduced it for the species she previously identified as *tenuiclavus* Zakhvatkin, 1941. The name *dimidiatus* has not been used so commonly in the United States, although Baker and Wharton (1952) recently applied it to the field species *oudemansi*.

Hermann's (1804) description of *dimidiatus*, in French, states:

"Abdomen spherical, of a yellowish green in front, white behind and underneath, with radiating hairs, longer than the body [this description is repeated in Latin], pl. VI, fig. 4. It is found among mosses. I have not observed any palp, but intermediary chelicerae (pl. IX, fig. b) which, however, were not articulated at all as in other mites".

There are a number of points in this description which, taken in conjunction with Hermann's drawings, suggest that it should not be accepted for any species of *Tyrophagus* at present known:

(1) *Form of the "abdomen"* [*i.e. the hysterosoma*].—Characteristically the hysterosoma of *Tyrophagus* is far from spherical as in Hermann's species, being longer than it is wide, with obvious "shoulders" anteriorly and flattened dorsoventrally (see Fig. 35, p. 166). In Hermann's illustration (pl. VI, fig. 4) of *dimidiatus*, too, there is a carefully drawn curving line across the hysterosoma which seems likely to represent either a colour boundary or an additional suture. Neither of these interpretations would be applicable to a species of *Tyrophagus*.

(2) *Colour.*—In all known species of *Tyrophagus* the body cuticle is colourless, with the legs and apodemes only slightly darkened. None of them has a characteristic distribution of yellowish green and white. Indeed any trace of colour in the hysterosoma could only be due to body contents showing through the cuticle, and would appear towards the posterior end, not anteriorly as Hermann described.

(3) *Habitat.*—Oudemans (1924*b*) does not appear to have been successful in finding his species in moss, the habitat recorded by Hermann, nor have species of *Tyrophagus* been found there by other authors.

(4) *Mouthparts.*—Hermann's description of the chelicerae appears to be the most significant statement of all. In the original French he referred to "des pinces intermédiaires, qui n'étoient cependant point articulées comme dans d'autres mites". But there is some doubt as to whether or not Hermann's illustration (pl. IX, fig. b) of the chelicerae is in agreement with his emphatic statement. If the written statement is accepted, then it must be assumed that Hermann's specimen was indeed one which lacked the articulation usual in other mites, and that the distally placed lines in his illustration were contour lines and not joints. If this view is taken, then *dimidiatus* must be excluded from the genus *Tyrophagus* on the basis of the structure of its chelicerae. Alternatively it may be accepted that Hermann's illustration represents a chelicera with normal articulation of the type found in *Tyrophagus*. But this interpretation does not agree with the written description, and non-agreement between the two would make the identification of *dimidiatus* impossible, and so would also constitute grounds for rejecting it as the name of a species of *Tyrophagus*.

Since the shape of the abdomen, the colour, the habitat, and the structure of the chelicerae are more characteristic of the Oribatei than the Sarcoptiformes, it seems possible that Hermann's species may have been one of the primitive "moss mites" rather than a *Tyrophagus*. On the grounds that all the above characteristics of *dimidiatus* point to some form other than *Tyrophagus*, and that, moreover, Hermann's description and illustration of the chelicerae must be interpreted either as direct evidence that the species is not a *Tyrophagus* or that it is a species which is beyond recognition, the suggestion is hereby put forward that the specific trivial name *dimidiatus* Hermann, 1804, be declared a *nomen dubium*. Notification of this suggestion, and of grounds on which it is made, are being placed before the International Commission on Zoological Nomenclature for a final decision.

Since it is considered here that *dimidiatus* should be rejected as a *nomen dubium*, *longior* Gervais becomes the first possible name for the economic species for which Oudemans used *dimidiatus*, and which has been so extensively recorded since, both in the present study and elsewhere. Gervais (1844) described his species as:

"*Tyroglyphe allonge* (*Tyroglyphus longior*) (pl. 35, fig. 5). Seconde espèce de mite, Lyonet, Mém. Mus., XVIII, 283, pl. 14, figs. 7–8. We have found this species living with the preceding on the crust of cheeses, called 'fromage de Gruyère' and 'de Hollande' ".

By this record, which conforms to the requirements of the International Rules of Zoological Nomenclature, *longior* can be accepted as an available name for the

species which Oudemans called *dimidiatus*. Subsequent to Gervais' description the species *longior* was clearly defined by illustrations published during the 19th century. In the plate of Fumouze and Robin (1867) the body form, particularly the relationship of tarsus length to body length, is so clearly illustrated that according to present knowledge of *Tyrophagus* it could represent only one species, and that the one which Oudemans renamed *dimidiatus*. Nalepa (1884–5) illustrates the male genital opening of the same species with such accuracy as to leave no doubt of its identity. Canestrini (1888) illustrates the penis, a character now recognized as one of the most valuable for the separation of species of *Tyrophagus*.

The conclusion is therefore reached that the same species which Gervais recorded as *longior* continued to be recognized under this name until Oudemans called it *dimidiatus** in error in 1924, and that the species is indeed correctly named *longior* (Gervais, 1844). It has been ascertained from the Muséum National d'Histoire Naturelle, Paris, that both Gervais' and Fumouze and Robin's material of *longior* is unknown and must be accepted as lost. Accordingly, to establish the species name beyond doubt, it is proposed to designate a neotype of *longior* (see p. 165), in this case from material collected in the course of the present study.

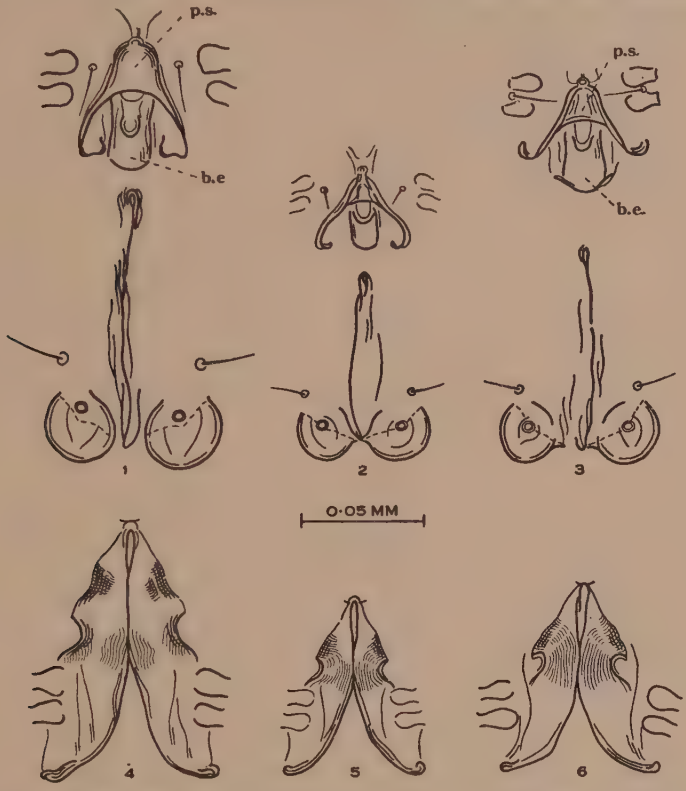
Oudemans was doubtful of the identity of *Tyroglyphus infestans*, which Berlese (1884) described as a new species although his illustrations indicate it to be *Tyrophagus longior*. In searching for Berlese's species Oudemans himself (1926) discovered a species not previously described, which he incorrectly named *T. dimidiatus* forma *infestans*. The same species was next described by Jary and Stapley (1937) under the name *Tyroglyphus dimidiatus* Hermann (*longior* Gervais). Zakhvatkin (1941) then used Oudemans' name *humerosus* for it. In each of these cases the species was incorrectly identified, and cannot therefore be recognized by any of the names applied to it. It is now necessary to describe it as a new species, for which the name *oudemansi* is proposed (see p. 167).

The present study suggests that the geographical distribution of the four clearly separable *Tyrophagus* species in the Oudemans Collection, now called *putrescentiae*, *palmarum*, *longior*, and *oudemansi*, is at least very wide indeed, and is probably truly cosmopolitan. Recently it has appeared that a fifth species, the *perniciosus* of Zakhvatkin (1941), may fall into the same category. Of the remaining 10 species which Oudemans placed in *Tyrophagus*, four (namely, *dimidiatus* forma *humerosus*, *dimidiatus* forma *longior*, *vanheurni*, and *viviparus*) are now considered to be synonyms of one or other of the above four species, three (*amboinensis*, *australasiae*, and *javensis*) are so closely related to *putrescentiae* that they may later have to be reduced in status at least to subspecies, while the remaining three are insufficiently defined and have had to be included in the list of Species Incertae Sedis (p. 174).

Although Oudemans examined the majority of the forms described under *Acarus* and *Tyroglyphus* during the 18th, 19th, and early 20th centuries for possible species of *Tyrophagus*, he appears to have ignored United States descriptions. There seems no doubt of the need to consider the species of Osborn (1893) and of Banks

* Oudemans (1906) had already used this name for a species collected in New Guinea, whose name he later changed to *putrescentiae* and later again (1916) to *australasiae*. This may account for the statement of Zakhvatkin (see p. 151).

(1906, 1917) as possible synonyms of European forms before accepting them as distinct. Within the past twenty years the Russian acarologists Zakhvatkin (1936, 1941), Volgin (1948, 1949), and Sorokin (1952) have added a number of new species to *Tyrophagus*, but some of these too require re-assessment in relation to earlier-described European species. From time to time, under both *Tyroglyphus* and *Tyrophagus*, further old species names are revived or new ones are erected for forms



Figs. 1–3.—Male genital opening and anus of: *Tyrophagus longior* (1), *T. palmarum* (2), and *T. putrescentiae* (3). Figs. 4–6.—Female genital opening of *T. longior* (4), *T. palmarum* (5), and *T. putrescentiae* (6). *b.e.*, basal element of penis; *p.s.*, penis support.

which undoubtedly belong to the latter genus and yet cannot be accepted with certainty as being other than one of the very widely distributed species referred to above. Such is the case with Seal and Eden's (1956) record of *Tyrophagus breviceps* (Banks), and Lombardini's (1944) description of *T. nadinus*, which he considered to be new.

Genus and Species Descriptions

Genus TYROPHAGUS Oudemans

Tyrophagus Oudemans, 1924*a*, p. 250.
Coelognathus Turk, 1953, p. 81.

Type species *Acarus putrescentiae* Schrank, 1781.

Body cuticle colourless, that of legs and apodemes sometimes darkened slightly. Propodosomal shield only weakly developed, but with characteristic curved outline. Well-developed exterior vertical hair (*v.e.*) arising laterally between chelicera and base of first leg. Internal scapulars (*sc.i.*) longer than externals (*sc.e.*). Dorsal setae (d_1, d_2) and lateral seta (*la*) short in relation to other hairs of hysterosoma. Principal body hairs long, flexible, either smooth or with minute pectinations only, 4–7 pairs forming a train at posterior end of body. Legs slender, extending well beyond lateral body margin. No spines developed laterally on legs, but at base of terminal caruncle 3 small spines borne ventrally, none dorsally. Grandjean's organ inconspicuous, main shaft simple, spiniform. Dorsally on tarsus I is a rod-like annulate seta or solenidion (ω_1) at about its own length from base, a microsense seta or famulus (ϵ) immediately in front of it, and on external surface a smaller solenidion (ω_2) of about a third its length. On tarsus II, in same position, the solenidion ω_1 only. Median setae *aa* and *ba* of tarsus I well developed, slender, flexible, placed on or near mid-dorsal line. On genual I internal apical solenidion σ_1 approximately $1\frac{1}{2}$ times as long as external apical solenidion σ_2. No marked sexual dimorphism. Male and female genital openings between bases of 3rd and 4th pairs of legs. Male genital opening in ventrodorsal view having penis support and basal element of penis separated into 2 units. Anus of female extending almost to posterior margin of body.

Key to Species of the Genus Tyrophagus

1. In dorsoventral view of male, arms of penis support turned inwards (Fig. 1); pseudostigmatic hair tapering evenly from base to tip, pectinations along most of its length (Fig. 10) 2

   In dorsoventral view of male, arms of penis support turned outwards (Fig. 3); pseudostigmatic hair either without pectinations, or with long pectinations only about its enlarged base (Figs. 29, 30) 7

2. Penis enlarged distally, tip obliquely truncate (Fig. 25) 3

   Penis of uniform diameter distally, or tapering, tip at right angles to longitudinal axis (Fig. 27) 4

3. Penis with distal half curving in opposite direction from proximal half; d_2 very short, usually about one-third to one-fourth length of chelicerae, always less than half their length (Fig. 38) ..... *oudemansi*, sp. nov.

   Penis curving in one direction only; d_2 approximately equal in length to chelicerae, or longer, always more than half their length (Fig. 40) ..... *perniciosus* Zakhvatkin

4. Dorsal hair d_2 approximately equal in length to anterior lateral hair *la*; pseudostigmatic hair straight, with long pectinations ..... *molitor* Zakhvatkin

   Dorsal hair d_2 $1\frac{1}{2}$–4 times as long as *la* (Fig. 35); pseudostigmatic hair curved, with short pectinations 5

5. In male, anus approximately equal in length to distance separating it from genital opening; the pair of male postanal hairs p_1 at same level as p_3, but themselves almost twice as far apart; p_1 long, little shorter than p_3 ..... *amboinensis* Oudemans

   In male, anus 6–18 times as long as distance separating it from genital opening; male postanal hairs p_1 anterior to p_3, only slightly further apart; p_1 short, one-quarter to one-third length of p_3 (Fig. 16) 6

6. d_2 $1\frac{1}{2}$-2 times length of *la*; in male, anus 17–18 times as long as distance separating it from genital opening ..... *longior* Gervais

   d_2 $3\frac{1}{2}$–4 times length of *la*; in male, anus 6–7 times as long as distance separating it from genital opening ..... *palmarum* Oudemans

7. Pseudostigmatic hair small, without pectinations; posterior lateral hair *lp* about one-third length of remaining posterior hairs ..... *brevicrinatus*, sp. nov.
   Pseudostigmatic hair large, with long pectinations about its enlarged base; *lp* approximately same length as remaining posterior hairs 8
8. d_2 equal to, or up to $1\frac{1}{2}$ times as long as, *la*; *la* rather long, extending beyond lateral body margin; penis bent once, bow-shaped ..... *tropicus*, sp. nov.
   d_2 $1\frac{1}{2}$–3 times as long as *la*; *la* short, not extending as far as lateral body margin; penis bent twice, S-shaped 9
9. Distance $a + b$ of male 4th tarsus $2\frac{1}{2}$–3 times as long as distance *c* ..... *australasiae* (Oudemans)
   Distance $a + b$ of male 4th tarsus $1\frac{1}{2}$–2 times as long as distance *c* (Fig. 21) 10
10. d_2 $1\frac{1}{2}$–2 times as long as *la*; distal half of penis shaft straight ..... *javensis* (Oudemans)
    d_2 2–3 times as long as *la*; distal half of penis shaft curved ..... *putrescentiae* (Schrank)

Tyrophagus putrescentiae (Schrank)

Figs. 3, 6, 9, 12, 15, 18, 21, 35

Acarus putrescentiae Schrank, 1781, p. 521.

Tyroglyphus subgen. *Tyrophagus putrescentiae* (Schrank, 1781), Oudemans, 1924*a*, p. 250; 1924*b*, p. xxiv.

Tyrophagus putrescentiae (Schrank, 1781), Womersley, 1941, p. 468, fig. 10; Zakhvatkin, 1941, p. 99; Nesbitt, 1945, p. 176, figs. 4, 16, 28; Hughes, 1948, p. 20; Baker and Wharton, 1952, p. 330.

Coelognathus putrescentiae (Schrank, 1781), Turk, 1953, p. 81.

Tyroglyphus lintneri Osborn, 1893, p. 360, fig. (unnumbered), syn. nov.; Banks, 1906, p. 15, figs. 23–25, 29.

Tyrophagus lintneri, Davis, 1944, p. 7, figs. 4–6; Baker and Wharton, 1952, p. 334.

Tyroglyphus americanus Banks, 1906, p. 16, figs. 20–22, syn. nov.

Tyroglyphus longior var. *castellanii* Hirst, 1912, p. 375, figs. 1, 2; Jary, 1937, p. 130.

Tyrophagus longior var. *castellanii*, Bollaerts and Breny, 1951.

Tyrophagus castellanii, Hughes, 1948, p. 21, figs. 14–20, syn. nov.; Baker and Wharton, 1952, p. 335.

Coelognathus castellanii, Turk, 1953, p. 81.

Tyroglyphus muscae Sasaki, 1921, syn. nov.; 1927, p. 151, figs. 8–11.

Tyrophagus vanheurni Oudemans, 1924*a*, p. 326, syn. nov.

Tyrophagus noxius Zakhvatkin, 1936, p. 25, syn. nov.; 1941, p. 103, figs. 36–38, 121, 125–131; Volgin, 1949, p. 385.

Tyrophagus bülleri Volostschuck, 1936, p. 155, syn. nov.

Tyroglyphus longior var. *taiwanensis* Sugimoto, 1938, p. 46, pl. 3, figs. 1–8, syn. nov.

Tyroglyphus nadinus Lombardini, 1944, p. 65, figs. 1, 2, syn. nov.

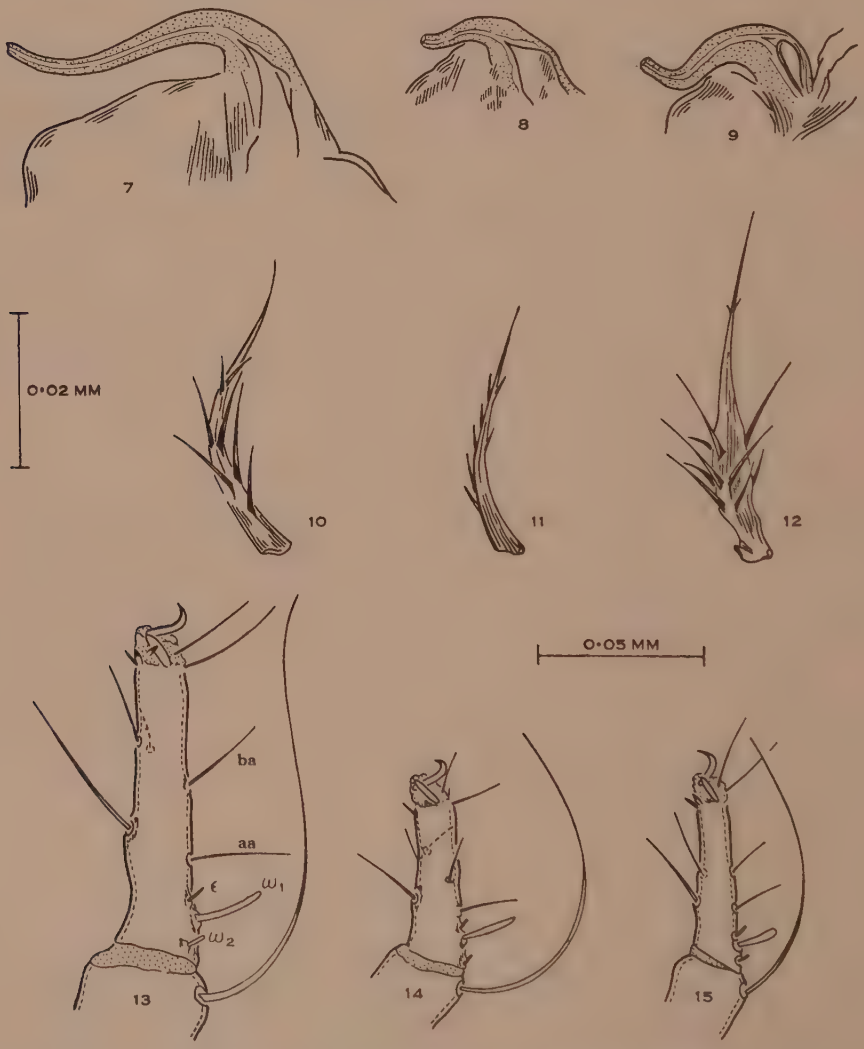
Neotype.—A male in the Oudemans Collection, Rijksmuseum van Natuurlijke Historie, Leiden, Catalogue No. 17, slide labelled "*Tyroglyphus putrescentiae* Schrank 1781, male dors. in humus Hilversum 22 April 1902 Oudemans". In addition to designating a neotype in the Oudemans Collection, one slide made during the present investigation, labelled "*Tyrophagus putrescentiae* (Schrank, 1781), 6♂♂, 11♀♀, ex cheese, Sutton Bonington, Leics., 20/10/50, P.L.R. Coll. No. 160(*b*)," has been deposited in the British Museum (Nat. Hist.), and another similarly labelled but with "2♂♂, 6♀♀" has been deposited in the Australian Museum, Sydney.

Male (*neotype*)

Internal and external humerals and scapulars and posterior laterals between 50 and 60 per cent. of body length. Hairs at posterior end of body, including 3rd

and 4th dorsals, from 85 to 95 per cent. of body length. Ratio of 2nd dorsal to anterior lateral (d_2/la) 2·03.

Ratio X/Y of distances between 1st and 3rd pair of postanal hairs 2·75. Bases of postanals almost in line, with 1st pair only a little in front of 3rd. Both 1st and 3rd postanals long, the 1st pair 23·3 per cent. of body length.



Figs. 7-9.—Penis of: *T. longior* (7), *T. palmarum* (8), and *T. putrescentiae* (9). Figs. 10-12.—Pseudostigmatic hair of: *T. longior* (10), *T. palmarum* (11), and *T. putrescentiae* (12). Figs. 13-15.—First tarsus of: *T. longior* (13), *T. palmarum* (14), and *T. putrescentiae* (15); *aa*, proximal dorsal median seta; *ba*, distal dorsal median seta; ϵ, famulus; ω_1, ω_2, basal solenidions.

Basal half of pseudostigmatic hair enlarged, bearing 3 rows of about 5 long pectinations; a few greatly reduced pectinations on distal half.

Solenidion ω_1 on 1st tarsus enlarged at tip. Origins of ω_1 and seta *aa* lying in mid-dorsal line from base to tip of tarsus, with seta *ba* displaced only slightly towards internal face.

Distance $a + b$, from base of 4th tarsus to distal margin of 2nd sucker, 1·78 times as long as c, the distance from latter point to tip of tarsus. One of hairs on opposite margin of tarsus arising almost at level of distal sucker, the 2nd above it and on its proximal side.

Penis support forming an inverted V, with arms straight and ends turning outwards; posterior margin of basal element of penis curved, almost completely filling space between arms. Penis small, bent twice (in form of S).

Anus 3·33 times as long as distance separating it from genital opening.

Dimensions.—Length of male neotype 349 μ; ratio of body length to length of 4th tarsus 6·23.

Female

As in the species described on the following pages, the female agrees with the male in dorsal hair relationships, form of the pseudostigmatic hair, and the arrangement of setae on the 1st tarsus. The form of the genital opening and arrangement of anal hairs are not sufficiently distinctive for species separation.

Habitat and Distribution Records

A. C. Oudemans Collection, Leiden.—In humus, Hilversum, 22.iv.1902; in stem groove of apple, Amsterdam, Apr. 1924; in tobacco seed, Medan, Deli, Indonesia, 1929; in rotten potatoes from Belgium, Wageningen, Netherlands, Feb. 1930; on dead *Tinea tinea*, Landesanstalt für Fischerei, Berlin, Dec. 1930; stem groove of *Citrus aurantium*, South Europe, Arnhem, Netherlands, Feb. 1932.

H. Vitzthum Collection, Munich.—Germany, 8.x.1924 (no habitat recorded).

School of Public Health and Tropical Medicine Collection, Sydney.—In *Paspalum* seed, Coopernook, N.S.W., 23.vii.1932; in "Vitaprotein" stock food, Sydney, 16.v.1939; in weevilly wheat, Sydney, Apr. 1941; from case of copra dermatitis, Sydney, Apr. 1942; on bacon, Riverstone, N.S.W., 22.x.1946; on jelly, Sydney, 25.ii.1946; in cage debris, Animal House, Sydney, 26.i.1950; on feed pellets, Animal House, Sydney, 1956; on Stilton cheese, Sydney, 5.v.1958.

Royal College of Veterinary Science Collection, Denmark.—From *Calandra* culture, Sept. 1943; from cockroach culture, 10.xii.1943; on ham, 25.i.1944.

H. H. J. Nesbitt Collection, Ottawa.—On rotting organic debris, Ottawa, 26.ix.1945.

United States National Museum Collection, Washington.—On onion, Brownsville, Mexico, 6.xii.1942; in old corn experiment, Georgia, 24.iv.1944; in *Heliconia mariae*, Barro Colo. Id., C.Z., May 1944; in shops and dwellings, Montgomery, Alabama, 20.iii.1945, Norfolk, Virginia, 16.v.1945, Loring, Virginia, 14.vii.1945, Arlington, Virginia, 1.vi.1945, Clarksville, Tennessee, 12.vii.1946, Kinston, N. Carolina, 27.viii.1946, Pensacola, Florida, 25.vi.1946, Corvallis, Oregon, 1.vi.1948, Alexandria, Virginia, 7.ix.1948, Washington, D.C., 6.vii.1950; on dead larvae of *Anacentrinus subnudus*, Baton Rouge, Louisiana, Feb. 1945; on *Gladiolus* corms, Cuernavaca, Mexico, 9.ii.1945, Orizaba, V.C., Mexico, 15.ii.1945, Mexico, D.F., 22.iii.1945, Mexico, D.F., 3.iv.1945; in stored rice, Crowley, Louisiana, 7.iii.1945; in *Coccolobis uvifera*, Homestead, Florida, 3.v.1945; in corn processing plant, Argo, Illinois, 18.vii.1945; in rat cages, College Park, Maryland, 12.ix.1945; on straw table mats, Corpus Christi, Texas, 13.ix.1945; on citrus leaves, Jalisco, Mexico, 3.i.1946; on beans, Modesto, California, 7.iv.1947; in cheese, Cartagena, Colombia, 9.v.1947; in thrip colony on oranges, Middleport, N.Y., 19.vi.1947; on orchid plants, Brownsville, Mexico, 23.vii.1947; on pineapple fruit, Isla, V.C., Mexico, 3.viii.1947; on cucumber leaf, greenhouse, Terre Haute, Indiana, 18.xi.1947; on mushrooms, St. Paul,

Minnesota, 1948; from ivy scale on sprouting potatoes, Riverside, California, 26.ii.1948; in Irish potato, Brownsville, Mexico, 7.v.1948; in cockroach cultures, Beltsville, Maryland, 14.vii.1949; on tomato, Brownsville, Mexico, 18.i.1950; on carpet from Haiti, Miami, Florida, 27.x.1950; in granary weevil culture, Wilmington, Delaware, 30.vi.1952; in bee pollen, Traverse City, Michigan, 1952; on bacon grease, Oxnard, California, 30.ix.1952.

P. L. Robertson Collection, Sydney.—On cheddar cheese, N. Taranaki, N.Z., 14.xii.1942, 17.xii.1942 (two factories), 19.xii.1942, 14.vi.1943; Manawatu, N.Z., 16.viii.1944; Toowoomba, Qld., Feb. 1947; on Australian cheddar cheese, Hayes, Middlesex, U.K., 9.x.1950; on English cheese, Reading, Berks., U.K., 11.x.1950, 2.xi.1950, 7.iii.1951; on English cheddar cheese, Sutton Bonington, Leics., U.K., 20.x.1950; on New Zealand cheddar cheese, Burwell, Cambs., U.K., 9.ii.1953, 9.iii.1953, 7.iv.1953, 27.vii.1953; in wool, Nelson, N.Z., 10.viii.1945; on dried Californian figs, Nelson, N.Z., 6.v.1946; on tomato relish, Nelson, N.Z., Sept. 1946; in Australian dried milk, U.K., 3.xi.1950; in laboratory culture of *Tenebrio molitor*, Pest Infestation Laboratory, (P.I.L.) Slough, Bucks., 18.iii.1952; on sultanas, P.I.L., 18.ix.1953; in ginger, P.I.L., Nov. 1953; on fungal culture, Indianapolis, U.S.A., 7.xii.1953; on marmalade, P.I.L., 28.vii.1954.

Tyrophagus amboinensis Oudemans

Tyrophagus amboinensis Oudemans, 1925, p. 33; 1927, p. 233, figs. 104–113.

Lectotype.—It is impossible to designate a lectotype of *amboinensis* as no material of the species was found in the Oudemans Collection, Rijksmuseum van Natuurlijke Historie, Leiden.

There appears little doubt that this species is distinct from any seen in the course of the present study. According to Oudemans' detailed description of 1927 it most closely resembles the *molitor* of Zakhvatkin.

General characteristics of *T. amboinensis* are its thickset appearance, small size, the smoothness of all its body hairs except the interior and exterior verticals and exterior scapulars, which are pectinate, and the ochreous yellow colour of the posterior half of the body. The following is based on the description and illustrations of Oudemans (1927):

Male

Ratio of 2nd dorsal to anterior lateral (d_2/la) approximately 1·9.

Ratio X/Y of distances between 1st and 3rd pair of postanal hairs 2·25. Bases of these two pairs of postanals in line across body; both pairs of hairs long.

Pseudostigmatic hair curved, long, basal half little enlarged and with rather short pectinations.

Solenidion ω_1 on 1st tarsus long, enlarged at tip. Solenidion ω_2 slender, long. Seta *aa* displaced from mid-dorsal line to external face of tarsus.

Genital aperture with penis support narrow, arms curving inwards, space between arms completely filled by large, curved basal element of penis. Penis medianly swollen, bent once through an angle of 180°, with distal part of shaft straight, rod-like.

Anus approximately equal in length to distance separating it from genital aperture.

Dimensions.—Length of male 268 μ; ratio of body length to length of 4th tarsus 8·56.

Habitat and Distribution Records.—Oudemans obtained his specimens from the island of Amboina, off the coast of Dutch New Guinea. He considered that they must have been accidentally introduced into the tube containing bat parasites, in which they were found, possibly before the parasites were collected.

Tyrophagus australasiae (Oudemans)

Tyroglyphus australasiae Oudemans, 1916, p. 267.

Lectotype.—Slide No. 8 of *T. australasiae* in the Oudemans Collection, Rijksmuseum van Natuurlijke Historie, Leiden, is hereby designated lectotype of the species. Eight of Oudemans' slides are referred to *australasiae* in the Leiden Collection, but only Nos. 7 and 8 are here accepted as belonging to it. Nos. 1–6 agree with *javensis*, and were obtained from the same locality and the same habitat (see p. 164).

It is possible that the status of *australasiae* may later have to be reduced to that of a subspecies, or even a race, of *putrescentiae*, but at the present stage of knowledge of *Tyrophagus* it must be retained as a separate species.

Oudemans separates *australasiae* from *putrescentiae* on the narrower "neck" region, smaller dimensions, broad lancet-form pseudostigmatic organ, and by the position of the suckers on the male 4th tarsus.

Dimensions.—Of two males mounted on the lectotype slide, *la* in one specimen is 38·64 μ in length, the ratio d_2/la is 2·66, and the ratio of the distance $a + b$, from base of 4th tarsus to distal margin of 2nd sucker, is 2·55 times as long as c, the distance from latter point to tip of tarsus. In the second specimen *la* is 31·08 μ, d_2/la is 2·30, and $(a+b)/c$ is 3·04.

Habitat and Distribution Records.—The two males on the lectotype slide were collected on the head of a crowned pigeon (*Goura* sp.) at Jamūr, New Guinea, on 6.viii.1903.

Tyrophagus brevicrinatus, sp. nov.

Figs. 24, 27, 30, 36

Holotype and allotype.—Collected by Miss P. Davey, Pest Infestation Laboratory, Slough, Bucks., mounted on slide deposited in the British Museum (Nat. Hist.), labelled "*Tyrophagus brevicrinatus* n. sp., ♂ holotype, ♀ allotype, +3♂♂, 2♀♀, 2 nymphs, ex copra, Takoradi, Gold Coast, 14.3.55. P.L.R. Coll. No. 246(2)". The male holotype and female allotype are indicated on this slide.

Paratypes.—One slide of 4♂♂, 4♀♀, and 2 nymph paratypes is deposited in the Australian Museum, Sydney.

Male (holotype)

Humerals, scapulars, 3rd and 4th dorsals, and posterior laterals shortened, stout, and pectinate, 18–21 per cent. of body length. Remaining hairs at posterior end of body approximately 50 per cent. of body length.

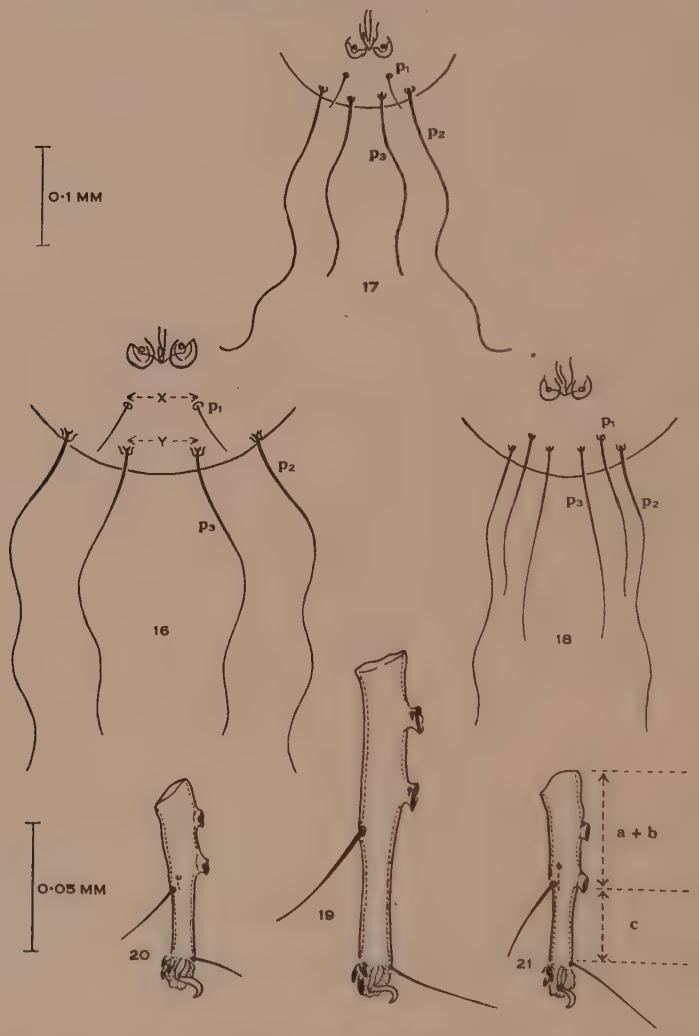
Anterior lateral hairs 38 μ long; ratio of 2nd dorsal to anterior lateral (d_2/la) 1·22.

Ratio X/Y of distances between 1st and 3rd pairs of postanal hairs 2·31. Bases of postanals in a line across body, and both pairs of hairs long.

Pseudostigmatic hair very small and smooth.

Solenidion ω_1 on 1st tarsus straight, slightly enlarged at tip.

Distance $a + b$, from base of 4th tarsus to distal margin of 2nd sucker, 2·02 times as long as c, the distance from latter point to tip of tarsus. One of hairs on opposite margin of tarsus arising almost at level of 2nd sucker.

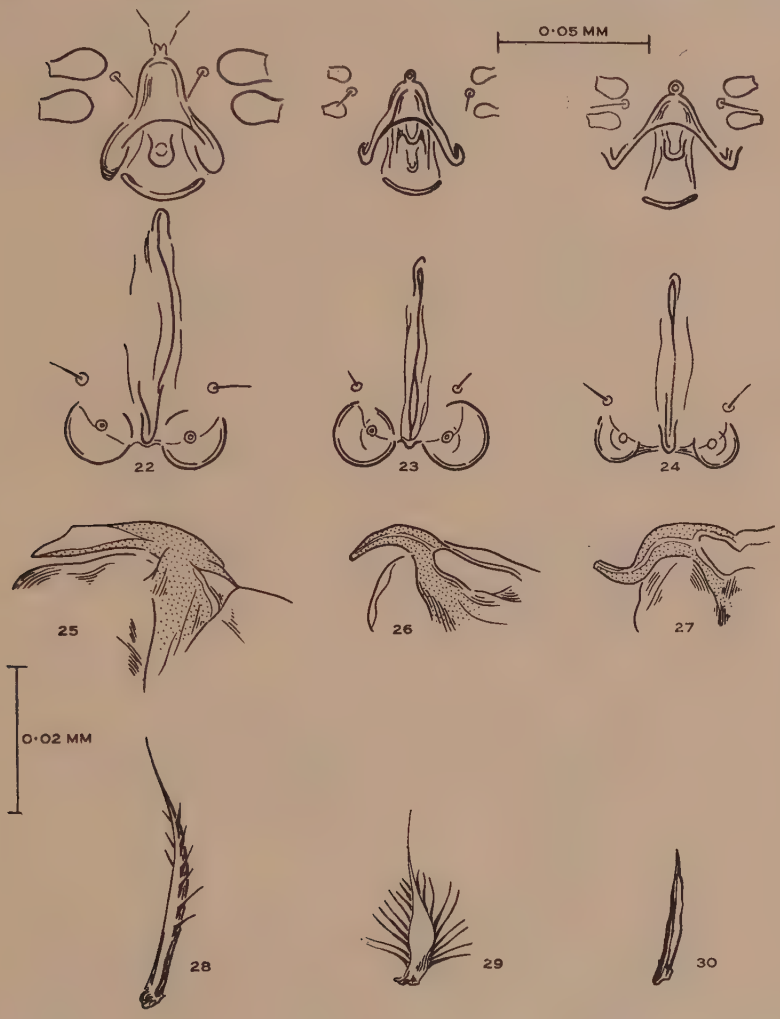


Figs. 16–18.—Male postanal setae of: *T. longior* (16), *T. palmarum* (17), and *T. putrescentiae* (18). Figs. 19–21.—Male 4th tarsus of: *T. longior* (19), *T. palmarum* (20), and *T. putrescentiae* (21). *X*, distance between 1st pair of male postanal setae; *Y*, distance between 3rd pair of male postanal setae; $a + b$, distance from base of 4th tarsus of male to distal margin of 2nd sucker; c, distance from distal margin of 2nd sucker to tip of male 4th tarsus (excluding claw); p_1, p_2, p_3, 1st, 2nd, and 3rd ventral postanal setae of male.

Penis support forming an inverted V, with ends turned outwards, but arms more widely separated than in *putrescentiae*; posterior margin of basal element

of penis curved, but not filling space between arms. Penis S-shaped as in *putrescentiae*. Anal suckers proportionally smaller than in *putrescentiae*, and more widely separated.

Anus 3·15 times as long as distance separating it from genital opening.



Figs. 22–24.—Male genital opening and anus of *T. oudemansi* (22), *T. tropicus* (23), and *T. brevicrinatus* (24). Figs. 25–27.—Penis of: *T. oudemansi* (25), *T. tropicus* (26), and *T. brevicrinatus* (27). Figs. 28–30.—Pseudostigmatic hair of: *T. oudemnasi* (28), *T. tropicus* (29), and *T. brevicrinatus* (30).

Dimensions.—Length of male holotype 457 μ; ratio of body length to length of 4th tarsus 8·31.

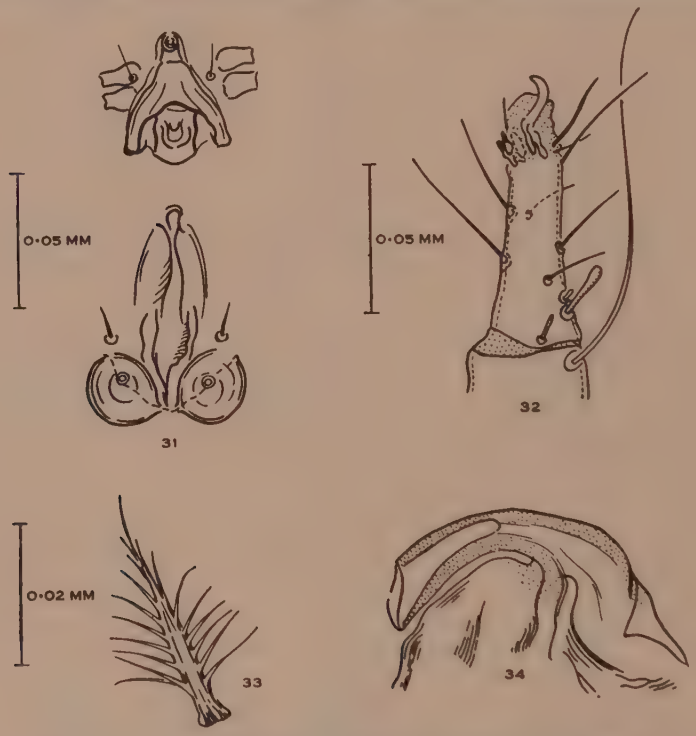
Habitat and Distribution Records.—Only the infestation from which the type material was mounted has so far been found.

Tyrophagus javensis (Oudemans)

Tyroglyphus javensis Oudemans, 1916, p. 267.

Lectotype.—Slide No. 6 of *Tyrophagus australasiae* in the Oudemans Collection, Rijksmuseum van Natuurlijke Historie, Leiden, is hereby designated the lectotype of *javensis*. The form of the penis, with the distal part of the shaft straight rather than curved as in *putrescentiae*, can be seen in this slide. Eight of Oudemans' slides—Nos. 1, 2, 3, 4, 5, and 6 of *australasiae* and Nos. 1 and 2 of *javensis*—are now considered to belong to the latter species.

T. javensis, like *T. australasiae*, may eventually have to be reduced in status to a subgroup of *putrescentiae*, but is at present being retained as a separate species.



Figs. 31–34.—*T. perniciosus*: male genital opening and anus (31), 1st tarsus (32), pseudostigmatic hair (33), penis (34).

Oudemans distinguishes *javensis* from *putrescentiae* by its longer and thicker hairs, broader and shorter "neck" region, by the form of the genital suckers, and of the pseudostigmatic organ.

Dimensions.—In one male specimen in the Oudemans Collection, *la* is 21·84 μ, d_2/la is 1·88, while the ratio of the distance $a + b$, from base of 4th tarsus to distal margin of 2nd sucker, is 1·64 times as long as c, the distance from the latter point to tip of tarsus. In a second male specimen *la* is 21·98 μ, d_2/la is 1·97, and $(a+b)/c$ is 1·83.

Habitat and Distribution Records.—Banjoewangi, Java, 1911; on eggs of the ant *Plagiolepis longipes*, Salatiga, Mar. 1915; in workings of *Plagiolepis longipes*, Salatiga, Mar. 1915.

Tyrophagus longior (Gervais)

Figs. 1, 4, 7, 10, 13, 16, 19, 37

Tyroglyphus longior Gervais, 1844, p. 262, pl. 35, fig. 5; Fumouze and Robin, 1867, p. 582, pl. 25; Nalepa, 1884–5, pls. 1, 2; Canestrini, 1888, p. 405, pl. 32, fig. 1; Canestrini and Kramer, 1899, p. 140; Banks, 1906, p. 14; Eales, 1918, p. 1088, figs. 1–3; André, 1933, p. 353, fig. (unnumbered).
Tyroglyphus dimidiatus forma *longior*, Oudemans, 1924*a*, p. 269.
Tyrophagus dimidiatus var. *longior*, Vitzthum, 1929, p. 75.
Tyrophagus longior, Hull, 1931, p. 40; Zakhvatkin, 1941, p. 109; Baker and Wharton, 1952, p. 335.
Tyroglyphus infestans Berlese, 1884 (p. and pl. unnumbered).
Tyrophagus dimidiatus var. *infestans*, Vitzthum, 1929, p. 75.
Tyrophagus infestans, Nesbitt, 1945, pp. 155, 159, 161, figs. 5, 17, 29, 40, 41.
Tyroglyphus dimidiatus (Hermann, 1804), Oudemans, 1924*a*, p. 269.
Tyroglyphus dimidiatus forma *dimidiatus*, Oudemans, 1924*a*, p. 269.
Tyroglyphus subgen. *Tyrophagus dimidiatus*, Oudemans, 1924*b*, p. xxv.
Tyrophagus dimidiatus, Vitzthum, 1929, p. 75.
Coelognathus dimidiatus, Turk, 1953, p. 81.
Tyroglyphus dimidiatus forma *humerosus*, Oudemans, 1924*a*, p. 269.
Tyrophagus dimidiatus var. *humerosus*, Vitzthum, 1929, p. 75.
Tyrophagus tenuiclavus Zakhvatkin, 1941, p. 109, figs. 86, 101–103, 153–158, syn. nov.; Hughes, 1948, p. 23, figs. 15–17, 19, 20; Volgin, 1949, p. 386; Bollaerts and Breny, 1951.
Coelognathus tenuiclavus, Turk, 1953, p. 81.

Neotype.—A male lodged in the British Museum (Nat. Hist.), and labelled "*Tyrophagus longior* (Gerv., 1844), ♂ dors., ex cheese, Gouda, Netherlands, 26.3.54. P.L.R. Coll. No. 237 (3, 4). Neotype". Two male specimens are mounted on the slide, the neotype being the one on the slide nearer the neotype label. One mounted female of the same population as the neotype, labelled "*Tyrophagus longior* (Gerv., 1844), ♀ dors., ex cheese, Gouda, Netherlands, 26.3.54. P.L.R. Coll. No. 237(23)" has also been deposited in the British Museum (Nat. Hist.). In addition, one male, "P.L.R. Coll. No. 237(19)", and one female, "P.L.R. Coll. No. 237(37)", from the same population as the neotype have been deposited in the Australian Museum, Sydney.

Male (*neotype*)

Internal and external scapulars and humerals between 40 and 45 per cent. of length of body; posterior laterals approximately 33 per cent. Hairs forming "train" at end of body from 85 to 95 per cent. of body length. Ratio of 2nd dorsal to anterior lateral (d_2/la) 1·53.

Ratio X/Y of distances between 1st and 3rd pair of postanal hairs 1·00. Distance separating the two pairs almost as great as that between hairs of each pair, so that bases lie at four corners of a square. First postanals only 8·03 per cent. of length of body, and considerably shorter than 3rd.

Pseudostigmatic hair curved, gradually tapering, bearing rather long pectinations along most of its length.

Solenidion ω_1 on 1st tarsus long, slightly curved, and tapering. Seta *aa* close to ω_1, with it and with *ba* forming a straight line to tip of tarsus.

Distance $a + b$, from base of 4th tarsus to distal margin of 2nd sucker 0·75 times as long as c, the remaining distance to tip of tarsus. Two hairs on opposite margin of tarsus lying well beyond level of distal sucker.

Penis support bell-shaped, with arms turned inwards at their posterior ends. Penis attenuated, shaft curved like spout of coffee pot.

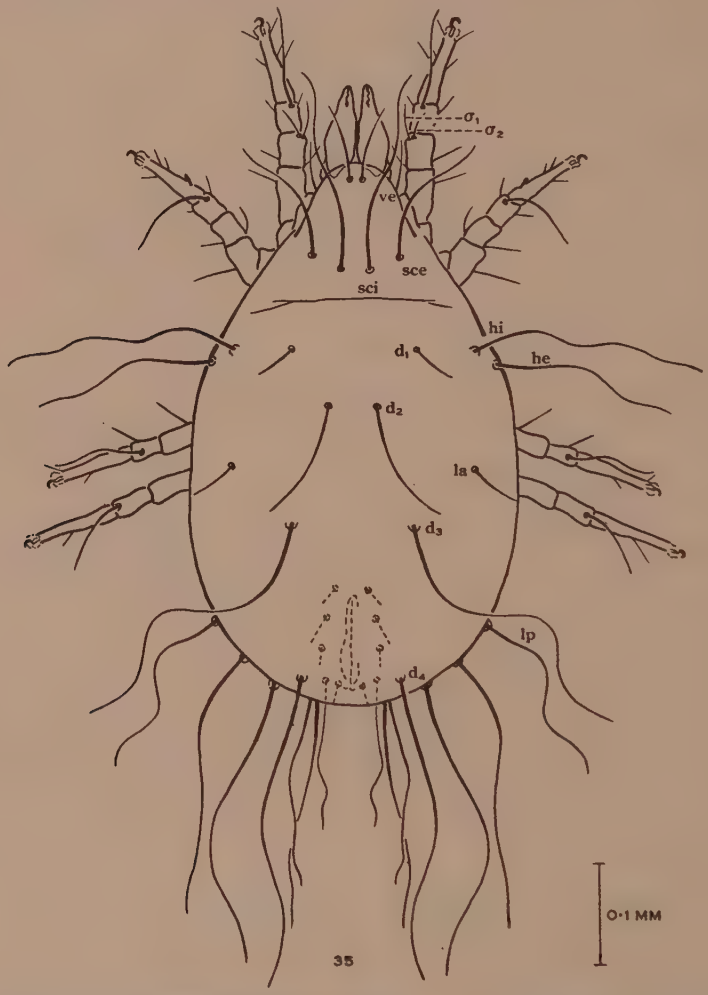


Fig. 35.—*T. putrescentiae*, female, dorsal; d_1, d_2, d_3, d_4, 1st, 2nd, 3rd, and 4th dorsal setae of hysterosoma; *hi*, *he*, internal and external humeral setae of hysterosoma; *la*, *lp*, anterior and posterior lateral setae of hysterosoma; *sci*, *sce*, internal and external scapular setae of propodosoma; *ve*, external vertical setae of propodosoma; σ_1, σ_2, internal and external apical solenidions of genual I.

Anus 17·97 times as long as distance separating it from genital opening.

Dimensions.—Length of male neotype 610 μ; ratio of body length to length of 4th tarsus 5·87.

Habitat and Distribution Records

A. C. Oudemans Collection, Leiden.—In house, Italy (coll. A. Berlese), 1901–02; on *Mus rattus* L., Arnhem, Netherlands, 8.x.1904; in fermenting tobacco, Puisflijk, Netherlands, 20.i.1917; in rotten weathered leaves, 1922; on cucumber and melon, Zwijndrecht, Netherlands, 20.v.1922; in grain commodities, Amsterdam, Oct. 1923; in hyacinth bulb, Sassenheim, Netherlands, Feb. 1924; in bark of *Ulmus* tree in *Scolytus* gallery, Oosterbeek, Netherlands, Jan. 1931; from cheese, Bremen, Germany (no date).

H. Vitzthum Collection, Munich.—Germany, 7.vii.1927, 25.ix.1936 (no habitats recorded).

Royal College of Veterinary Science, Denmark.—Denmark, Oct. 1907 (no locality, no habitat recorded); on mushrooms, Kastrup, Suhr, 10.xii.1929.

H. H. J. Nesbitt Collection, Ottawa.—Ex grain debris, boat, Montreal, Quebec, 21.x.1941.

P. L. Robertson Collection, Sydney.—On cheddar cheese: N. Taranaki, N.Z., 14, 17, 19.xii.1942 (two factories), 14.vi.1943, 23.viii.1944; Southland, N.Z., 9.iii.1944 (two factories); Manawatu, N.Z., 16.viii.1944 (two factories), Wairarapa, N.Z., 17.viii.1944; Melbourne, 26.vi.1945; Brisbane, Feb. 1947. On Australian cheddar cheese: Hayes, Middlesex, 9.x.1950; Wells, Somerset, 5.xii.1950; Westbury, Wilts., 8.xii.1950. On Stilton cheese: Long Clawson, Leics., 19.x.1950; Hartington, Derbyshire, 20.x.1950. On English cheddar cheese: Wells, Somerset, 5.xii.1950; Crewkerne, Somerset, 7.xii.1950; Westbury, Wilts., 8.xii.1950. On New Zealand cheddar cheese: Wells, Somerset, 5.xii.1950; Burwell, Cambs., 19.viii.1952, 10.i.1953, 9.ii.1953, 9.iii.1953, 7.iv.1953, 27.vii.1953. On Dutch cheese: Gouda, Netherlands, 26.iii.1954; Meppel, Netherlands, 5.iv.1954. In Ryegrass seed, Timaru, N.Z., 12.iv.1946; in red clover in the field, Waimate, N.Z., 15.iv.1946; on ham, Melton Mowbray, Leics., 8.xi.1950; in wheat, Holbeach St. Johns, Lincs., 16.x.1954, in hay, Reepham, Norfolk, 18.viii.1955.

Tyrophagus molitor Zakhvatkin

Tyrophagus molitor Zakhvatkin, 1941, p. 106, figs. 137–141.

Type.—Two males from refuse under wooden flooring in yard of flour mill, Saratov, Russia (designated by Zakhvatkin and presumably retained in his collection).

This species has not been found during the present investigation, and no record of its occurrence outside Russia has been traced.

Zakhvatkin places it closest to *perniciosus*, but separates it from the latter on the d_2/la ratio (which is approximately 1 : 1), on the enlarged egg-shaped famulus ϵ (β sensillum according to Zakhvatkin) on tarsus I, and on the penis, which is small, with blunt, rounded end, almost straight, but with slight indications of the two bends characterizing *putrescentiae* and *longior*.

The female is unknown.

Tyrophagus oudemansi, sp. nov.

Figs. 22, 25, 28, 38

Tyroglyphus dimidiatus forma *infestans* (Berlese, 1884), Oudemans, 1924*a*, p. 269.

Tyrophagus infestans Berlese, 1884, Oudemans, 1926, p. 144.

Tyroglyphus dimidiatus Hermann (*longior* Gervais), Jary and Stapley, 1937, p. 119, 5 figs.; van den Bruel, 1940, p. 87, fig. 3.

Tyrophagus dimidiatus var. *dimidiatus* (Hermann), Nesbitt, 1945, p. 155.

Tyrophagus dimidiatus (Hermann), Baker and Wharton, 1952, p. 335.

Tyrophagus humerosus (Oudemans, 1923), Zakhvatkin, 1941, p. 106, figs. 89, 142–152; Sorokin, 1952, p. 545.

Holotype and allotype.—Collected by W. I. St. G. Light, National Agricultural Advisory Service, Wye, Kent, mounted on slide labelled "*Tyrophagus oudemansi* n. sp., ♂ holotype, ♀ allotype, + 1♂, 5♀♀, ex mushrooms, Wye, Ashford, Kent, 5.3.51. P.L.R. Coll. No. 184(1)", deposited in the British Museum (Nat. Hist.). The male holotype and female allotype are indicated on this slide.

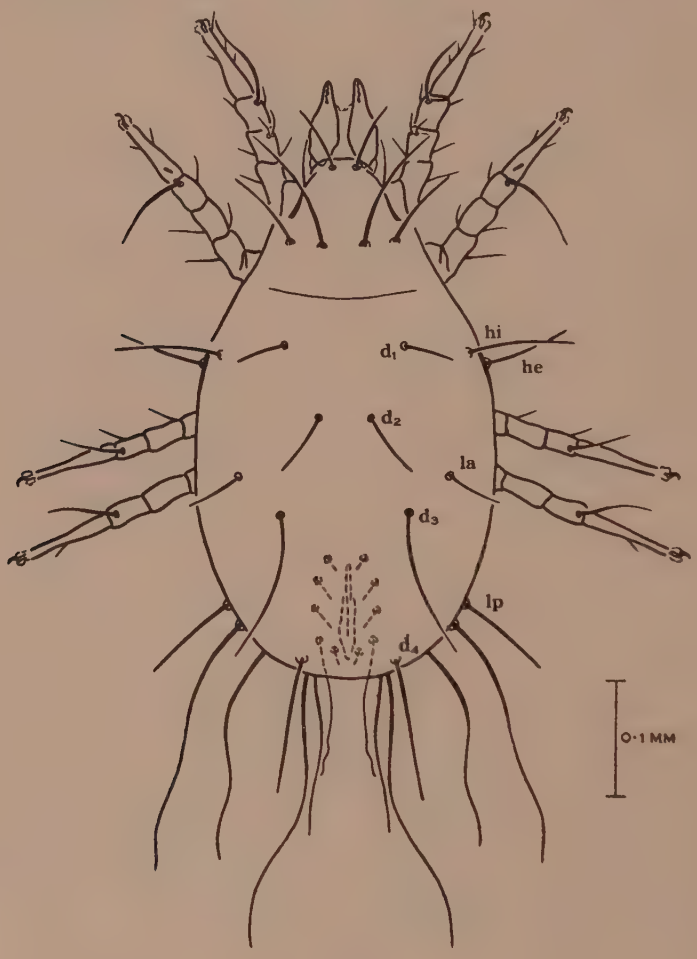


Fig. 36.—*T. brevicrinatus*, female, dorsal. Lettering as for Figure 35.

Paratypes.—A slide of 2♂♂ and 9♀♀ paratypes, P.L.R. Coll. No. 184(4), has been deposited in the Australian Museum, Sydney.

Male (*holotype*)

Internal and external humerals and scapulars, and posterior laterals 35–45 per cent. of body length. Hairs at posterior end of body 65–75 per cent. of body length. Ratio of 2nd dorsal to anterior lateral (d_2/la) 1·12.

First and 2nd dorsals and anterior laterals very short, about 16–18 μ, and fine.

Ratio X/Y of distances between 1st and 3rd pair of postanal hairs 1·17. First pair of male postanals short, arising anterior to 3rd pair, and separated by approximately the same distance.

Pseudostigmatic hair slender and curved, with rather short pectinations along its length.

Solenidion ω_1 on 1st tarsus clubbed at tip.

Distance $a + b$ of male 4th tarsus 1·02 times as long as c. The 2 hairs on opposite margin of tarsus arising about level of distal sucker.

Posterior arms of penis support turned inwards; basal element of penis enlarged posteriorly. Penis only slightly curved, broadened towards tip, obliquely truncate.

Anus 19·54 times as long as distance separating it from genital opening.

Dimensions.—Length of male holotype 483 μ; ratio of body length to length of 4th tarsus 6·19.

Habitat and Distribution Records

A. C. Oudemans Collection, Leiden.—Damaging seedling plants of rye and barley, Landsberg, Germany, 6.x.1925; in rye and barley, Landsberg, Germany, Oct. 1925; seedling plants of *Lycopersicon esculentum*, Rotterdam, 15.xi.1937.

School of Public Health and Tropical Medicine Collection, Sydney.—Ex straw, plant nursery, Sydney, May 1954.

P. L. Robertson Collection, Sydney.—On Iceland poppy plants, Waikanae, N.Z., 22.v.1946; in soil and grass, Nelson, N.Z., 7.ii.1947; on mushrooms, Wye, Kent, U.K., 5.iii.1951; on petunia seedlings, Wye, Kent, 4.v.1951; from soil of insect culture, Cambridge, U.K., 15.vii.1952.

Tyrophagus palmarum Oudemans

Figs. 2, 5, 8, 11, 14, 17, 20, 39

Tyroglyphus subgen. *Tyrophagus palmarum* Oudemans, 1924*b*, p. xxvi.
Tyrophagus viviparus Oudemans, 1926, p. 146, syn. nov.
Tyrophagus longior (Gervais, 1844), Robertson, 1946, p. 198, figs. 16, 17.
Tyrophagus parvulus Volgin, 1949, p. 388, figs. 2, 4, syn. nov.
Tyrophagus dimidiatus infestans (Berlese), Bollaerts and Breny, 1951.

Lectotype.—A male in the Oudemans Collection at the Rijksmuseum van Natuurlijke Historie, Leiden, Catalogue No. 1, slide labelled "rotte kamerpalmstronk Arnhem. Octob. 1923. Oudemans. Male, Female, Nph. III dors. vent. lat." Of the material studied during the present investigation one slide of two males and one of two females labelled respectively "*Tyrophagus palmarum* Oudemans, 1924, ♂ dors., ex Welsh Cheddar in store, Westbury, Wilts., 8.12.50, P.L.R. Var. Ser. III (13, 14)" and "*Tyrophagus palmarum* Oudemans, 1924, ♀ dors. . . . . P.L.R. Var. Ser. III (85, 86)" have been deposited in the British Museum (Nat. Hist.). In addition, two males, "P.L.R. Var. Ser. III (9, 10)," and two females, "P.L.R. Var. Ser. III (57, 58)," of the same population as the foregoing, have been deposited in the Australian Museum, Sydney.

Male (*typical specimen*)

Internal scapulars, humerals, and posterior laterals 40–50 per cent. of body length; posterior hairs approximately 70 per cent. Ratio of 2nd dorsal to anterior lateral (d_2/la) 3·57.

First pair of postanal hairs considerably further forward than 3rd pair; ratio of distances between bases of 1st and 3rd pairs 1·3. First postanal short, about 9·65 per cent. of body length.

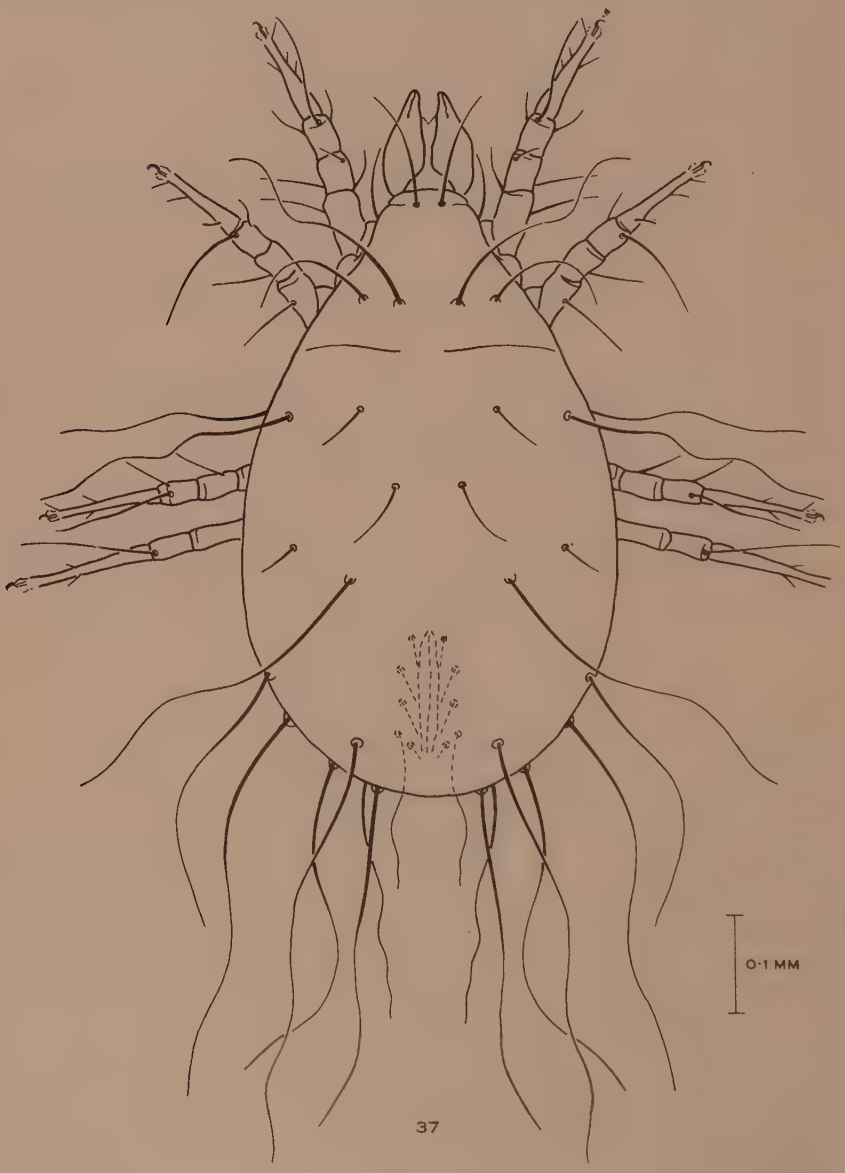


Fig. 37.—*T. longior*, female, dorsal.

Pseudostigmatic hair small, slightly curved, with short pectinations from base to near tip.

Solenidion ω_1 on 1st tarsus straight and slightly enlarged about the centre. Seta *ba* moved towards internal surface of tarsus from position held in *putrescentiae* and *longior*.

Fourth tarsal distance $a + b$ 1·27 times remainder of tarsus c; the 2 setae on ventral side of tarsus arising at level of distal sucker.

Lateral arms of penis support curved and widely extended, with ends turning inwards. Penis short, blunt, but shaft with double curve as in *putrescentiae* and *longior*.

Ratio of length of anus to distance separating it from genital opening 6·8.

Dimensions.—Length of male specimen described 487 μ; ratio of body length to length of 4th tarsus 8·12.

Habitat and Distribution Records

A. C. Oudemans Collection, Leiden.—Rotten stalk of indoor palm, Arnhem, Oct. 1923.

P. L. Robertson Collection, Sydney.—On cheddar cheese: N. Taranaki, N.Z., 14.vi.1943, 23.viii.1944; Marlborough, N.Z., 3.ii.1944, 15.iii.1944, 23.ii.1945; Southland, N.Z., 9.iii.1944 (three factories); Manawatu, N.Z., 17.viii.1944; Wairarapa, N.Z., 17.viii.1944 (three factories). On Stilton cheese: Long Clawson, Leics., 19.x.1950. On English cheddar cheese: Wells, Somerset, 5.xii.1950; Wedmore, Somerset, 6.xii.1950; Westbury, Wilts., 8.xii.1950. On Australian cheddar cheese: Wells, Somerset, 5.xii.1950; Westbury, Wilts., 8.xii.1950. On Welsh cheddar cheese: Westbury, Wilts., 8.xii.1950. On cheese made in Chile, 11.viii.1951; on New Zealand cheddar cheese, Burwell Cambs., U.K., 10.i.1953, 9.ii.1953, 9.iii.1953, 7.iv.1953, 27.vii.1953; on cheese, Gouda, Netherlands, 26.iii.1954; on ham, Melton Mowbray, Leics., 8.xi.1950; on Turkish sultanas, U.K., 28.ii.1951; on hay, Bletchingley, Surrey, 15.x.1954.

Tyrophagus perniciosus Zakhvatkin

Figs. 31, 32, 33, 34, 40

Tyrophagus perniciosus Zakhvatkin, 1941, p. 104, figs. 83, 132–136.

Type.—Not recorded by Zakhvatkin.

Male (typical specimen)

Internal humerals, internal scapulars, and posterior laterals 40–45 per cent., external humerals and scapulars 20–30 per cent. of body length. Third and 4th dorsals and other posterior hairs forming a train 60–80 per cent. of body length. Ratio of 2nd dorsal to anterior lateral (d_2/la) 3·90.

First pair of postanal hairs considerably nearer to anal suckers than 3rd pair. Ratio X/Y of distances between bases of 1st and 3rd pair 1·61. First postanals shorter than 3rd, only 6·61 per cent. of body length.

Pseudostigmatic hair straight, tapering gradually, with 2 lateral rows of 6–9 pectinations diminishing in size distally.

Solenidion ω_1 on 1st tarsus rather stout, clubbed at tip. Seta *aa* displaced towards external surface of tarsus, but close to famulus ϵ, seta *ba* placed dorsally towards internal surface.

Distance $a + b$, from base of 4th tarsus to distal margin of 2nd sucker, 1·44 times as long as c, the distance from latter point to tip of tarsus. Hairs on opposite margin about same level as distal sucker, slightly nearer base of tarsus.

Arms of penis support curved, with ends turned inwards; basal element of penis narrow, only half filling space between arms. Penis large, curved in one direction only, enlarged towards tip, obliquely truncate.

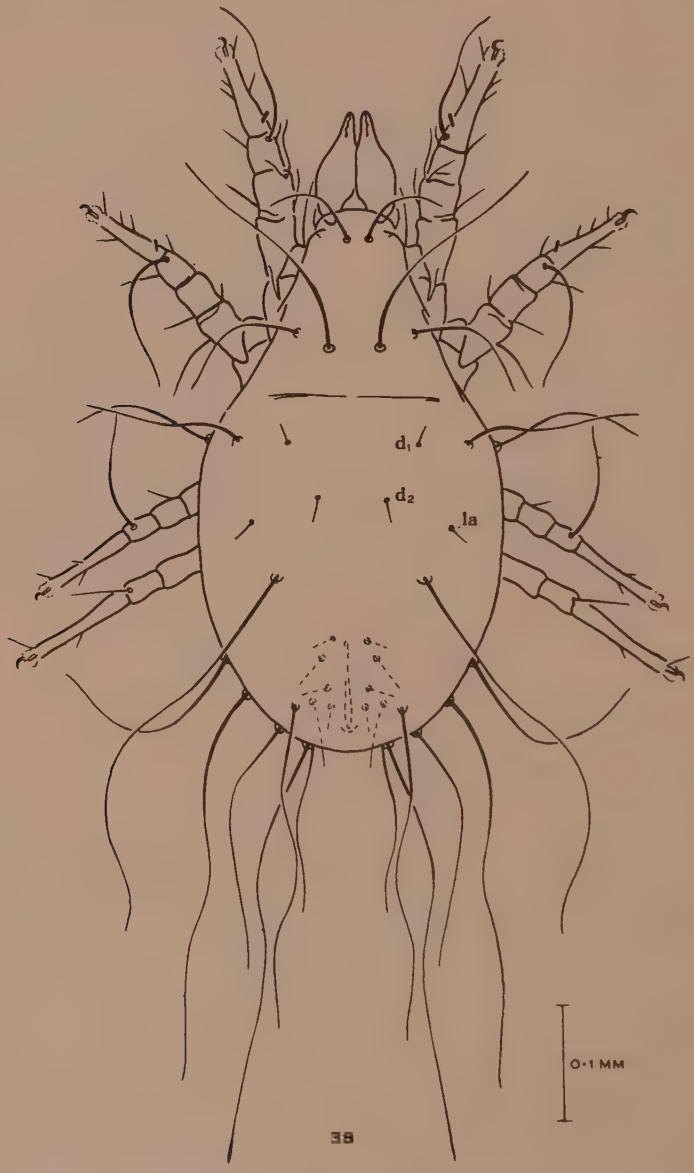


Fig. 38.—*T. oudemansi*, female, dorsal. Lettering as for Figure 35.

Anus 5·6 times as long as distance separating it from genital opening.

Dimensions.—Length of typical male specimen 521 μ; ratio of body length to length of 4th tarsus 7·37.

Habitat and Distribution Records.—On oats and barley in the field, in granaries and storehouses, Kostroma, Barnaul, many places in districts of Krasnodar and Ordshonikidse, U.S.S.R. (according to Zakhvatkin); on old, damaged cheese, Liverpool area, U.K., 1953 (mimeographed Technical Circular 1952–3, Infestation Control Division, Ministry of Agriculture and Fisheries); in dirty seed in budgerigar cage, Adelaide, 18.xi.1957 (per H. Womersley).

Tyrophagus tropicus, sp. nov.

Figs. 23, 26, 29, 41

Holotype.—Male mounted on slide deposited in the British Museum (Nat. Hist.), labelled "*Tyrophagus tropicus* n. sp., holotype ♂, +1♂, ex palm kernel dust, Lagos, Nigeria, 31.10.51, P.L.R. Var. Ser. X (9, 10)". The holotype is indicated on this slide.

Allotype.—Female of the same population on slide labelled ". . . . . allotype ♀, + 1 ♀, ... P.L.R. Var. Ser. X (49, 50)", also deposited in the British Museum (Nat. Hist.).

Paratypes.—One slide of 2 ♂♂ and one of 2 ♀♀ paratypes, "P.L.R. Var. Ser. X (17, 18)" and "P.L.R. Var. Ser. X (57, 58)" respectively, have been deposited in the Australian Museum, Sydney.

Male (*holotype*)

Internal and external humerals and scapulars, and posterior laterals, between 25 and 35 per cent. of body length. Hairs at posterior end of body from 40 to 60 per cent. of body length.

Anterior lateral hairs conspicuously lengthened beyond body margin, from 60 to 70 μ in length. Ratio of 2nd dorsal to anterior lateral (d_2/la) 1·06.

Ratio X/Y of distances between 1st and 3rd pairs of postanal hairs 1·71. Bases of postanals forming a curved line with 1st pair a little in front of 3rd. Both 1st and 3rd postanals long, but 3rd pair conspicuously longer than 1st.

Pseudostigmatic hair resembling that of *putrescentiae*, but with base more bulbous and tip tapering more finely.

Solenidion ω_1 on 1st tarsus long, slender, and slightly enlarged at tip.

Ratio $(a + b)/c$ of 4th tarsus of male similar to that of *putrescentiae*, measuring 1·82 in holotype.

Penis support forming an inverted V with ends turned outwards, but with arms more closely approximated than in *putrescentiae*. Penis very short and scarcely curved.

Anus 2·51 times as long as distance separating it from genital opening.

Dimensions.—Length of male holotype 432 μ; ratio of body length to length of 4th tarsus 9·19.

Habitat and Distribution Records.—In tobacco, Jacquinot Bay, New Britain, August 1945; in palm kernel dust, Lagos, Nigeria, 31.x.1951; on copra, Zanzibar, March 1952; in native-cleaned rice, Accra, Gold Coast, December 1952.

Tyrophagus vanheurni Oudemans

Tyrophagus vanheurni Oudemans, 1924*a*, p. 326.

Lectotype.—The male on slide No. 6 of *T. vanheurni* in the Oudemans Collection, Rijksmuseum van Natuurlijke Historie, Leiden, is hereby designated lectotype.

According to material preserved in the Oudemans Collection, this species has no status. Oudemans' specimens are a mixture of *palmarum* and *putrescentiae*. With the designation of a lectotype it becomes possible to list *vanheurni* as a synonym of *putrescentiae* (see p. 157).

Habitat and Distribution Records.—Material mounted on the lectotype slide and on the other six slides which Oudemans placed under *vanheurni* was all collected from a coconut, at Twello, Netherlands, in March 1924.

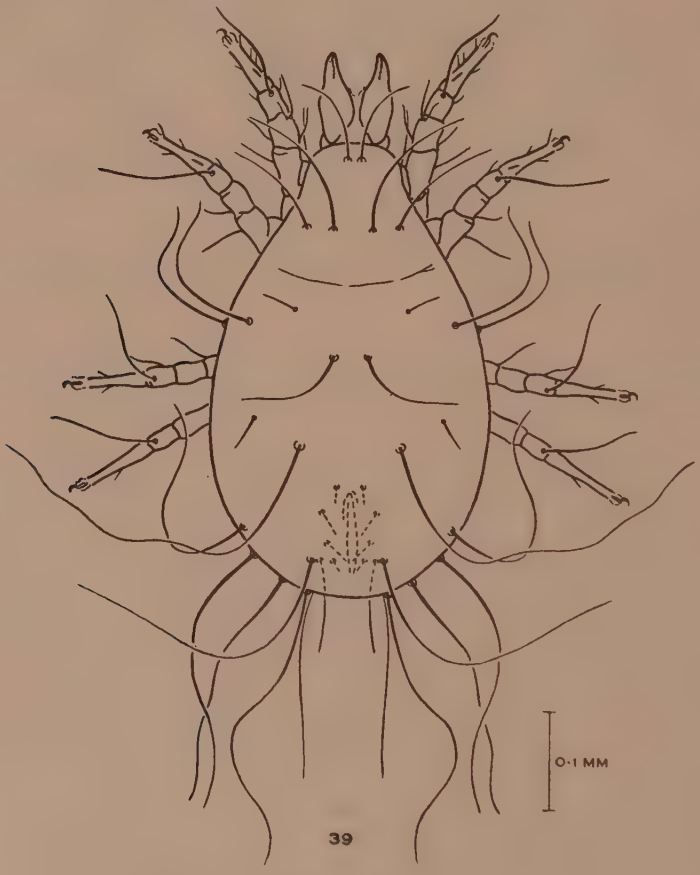


Fig. 39.—*T. palmarum*, female, dorsal.

SPECIES INCERTAE SEDIS

Tyrophagus breviceps (Banks)

Tyroglyphus breviceps Banks, 1906, p. 14.

The species recorded under this name by Seal and Eden (1956) is most likely to be either *putrescentiae* or *longior*. Banks described the species originally from dead larvae of the cotton boll weevil, but no characters were included on which to distinguish it from other known forms.

Tyrophagus cocciphilus (Banks)

Tyroglyphus cocciphilus Banks, 1906, p. 16.

This form was found with *Lecanium* on plum, with oyster-shell scale on orange, and with mealy bug on guava in U.S.A. Banks suggested that it might be only a variation of *lintneri* (i.e. of *putrescentiae*).

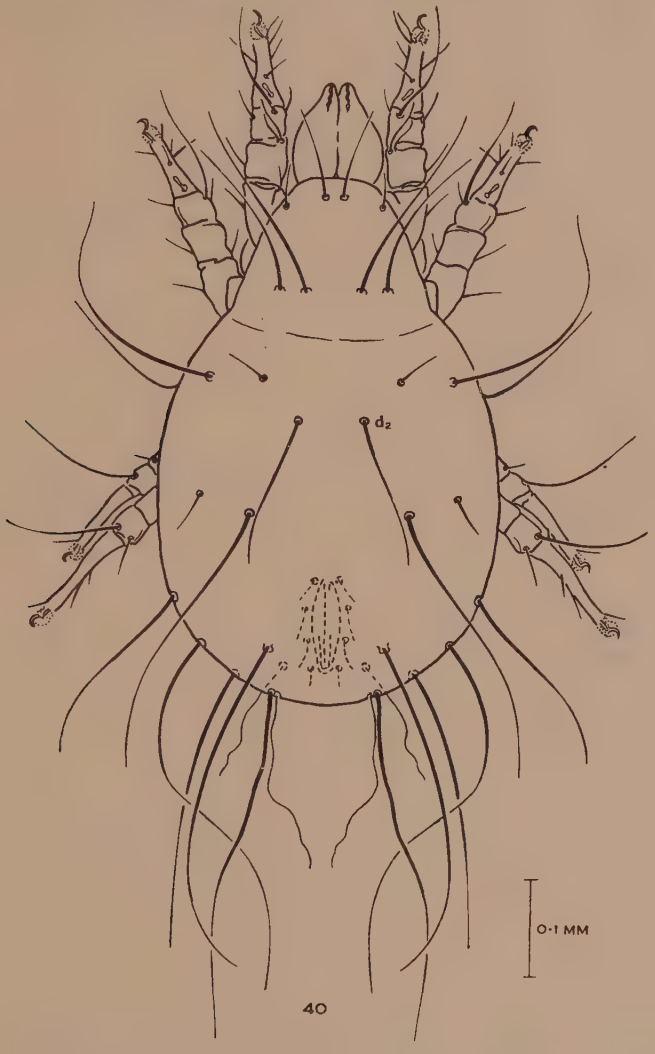


Fig. 40.—*T. perniciosus*, female, dorsal; d_2, 2nd dorsal seta of hysterosoma.

Tyrophagus deliensis (Oudemans)

Tyroglyphus deliensis Oudemans, 1923, p. 208.

Oudemans illustrated only the female of this species and only females are held in the Oudemans Collection, so that with the material available it cannot be defined adequately.

Lectotype.—The female on slide No. 2 of *T. deliensis* in the Oudemans Collection, Leiden, is hereby designated lectotype.

Tyrophagus formicetorum Volgin

Tyrophagus formicetorum Volgin, 1948, p. 509.

This is smaller than the typical *perniciosus*, but no other obvious differences can be found. It agrees also with *vjatscheslavi* Sorokin, 1952, from the same habitat of ants nests.

Tyrophagus karamani? Oudemans

Tyrophagus karamani Oudemans, 1933, Buitendijk, 1945, p. 354.

This form is represented in the Oudemans Collection, Leiden, by one slide dated 1929 and two plates of illustrations dated 1923, but Oudemans' 1933 description, cited by Buitendijk (1945), is of an Opilion, not a *Tyrophagus*. No authentic published description of *T. karamani* can be traced.

Tyrophagus mixtus Volgin

Tyrophagus mixtus Volgin, 1948, p. 511.

The species is somewhat similar to *oudemansi*, although some hairs such as *lp* are proportionally longer. There is nothing sufficiently definitive to warrant recognizing it as a distinct species.

Tryophagus muris Oudemans

Tyrophagus muris Oudemans, 1924*a*, p. 270.

There are no distinctive characteristics for separation from other known species.

Lectotype.—The female on slide No. 1 of *T. muris* in the Oudemans Collection, Leiden, is hereby designated lectotype.

Tyrophagus oblongulus (Koch)

Tyrophagus oblongulus (C. L. Koch VII, 1841), Oudemans, 1939, p. 185.

Koch's species was not thought to be identifiable by Michael (1903), but Oudemans first thought it to be *Acarus siro* L. and later placed it in *Tyrophagus*.

Tyrophagus sacchari (Banks)

Tyroglyphus sacchari Banks, 1917, p. 198.

The description and figures have not been seen by the author, and the species is left as uncertain on this ground.

Tyrophagus similis Volgin

Tyrophagus similis Volgin, 1949, p. 387.

The characters described are too variable to be definitive. The species is very close to *oudemansi*.

Tyrophagus vjatscheslavi Sorokin

Tyrophagus vjatscheslavi Sorokin, 1952, p. 545.

This species was obtained from ants nests, Russia, and like *formicetorum* is close to, or identical with, *perniciosus*.

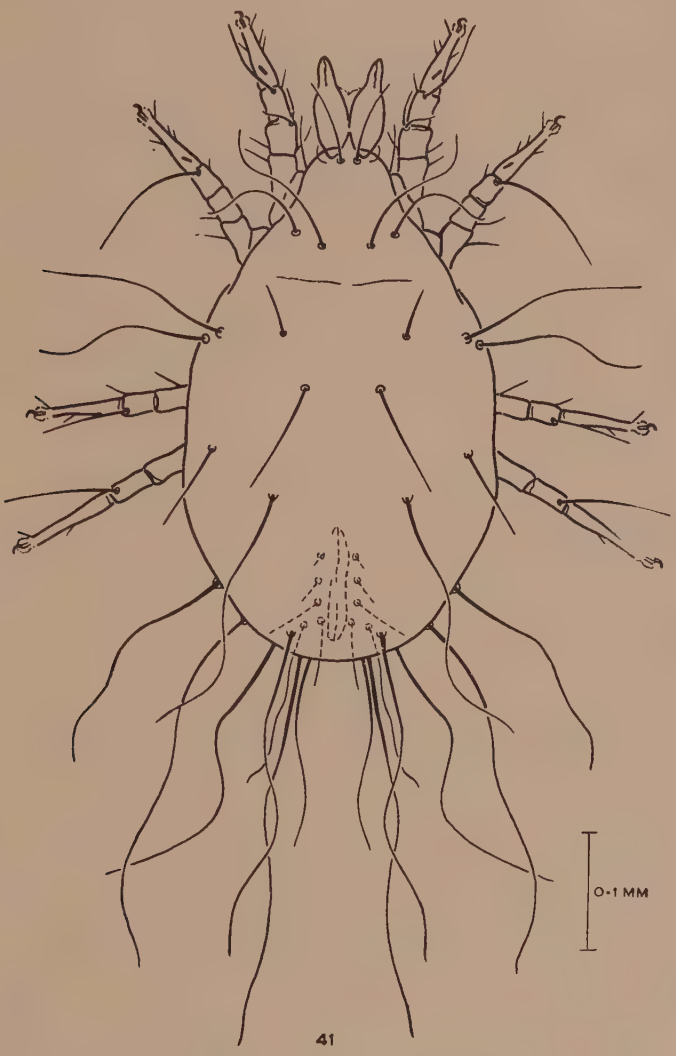


Fig. 41.—*T. tropicus*, female, dorsal.

Tyrophagus vjatskensis Sorokin

Tyrophagus vjatskensis Sorokin, 1952, p. 542.

Also collected from ants nests, Russia, this species is close to, or identical with, *longior*.

Tyrophagus zachvatkini Volgin

Tyrophagus zachvatkini Volgin, 1948, p. 510.

The species, like *vjatskensis*, appears to be very close to, or identical with, *longior*.

Acknowledgments

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References

André, M. (1933).—Notes sur les Acariens observés dans les magasins régionaux de tabacs. *Ann. Épiphytol.* **19**: 331–56.

André, M. (1949).—Ordre des Acariens. In "Traité de Zoologie". (Ed. P. Grassé.) (Paris.)

Baker, E. W., and Wharton, G. W. (1952).—"An Introduction to Acarology." (The MacMillan Company: New York.)

Banks, N. (1906).—A revision of the Tyroglyphidae of the United States. Tech. Ser. U.S. Bur. Ent. No. 13.

Banks, N. (1917).—New mites, mostly economic. *Ent. News* **28**: 193–9.

Berlese, A. (1884).—"Acari, Miriapodi e Scorpioni Italiani (Acari, Myriapoda et Scorpiones hujusque in Italia reperta)." Fasc. 14. No. 6. (Padua.)

Berlese, A. (1897).—"Acari, Miriapodi e Scorpioni Italiani, Ordo Cryprostigmata." Fasc. 14. No. 6. (Portici.)

Bollaerts, D., and Breny, R. (1951). Les Acariens nuisibles aux matières entreposées. *Rev. Agric., Brux.* **4**(6): 738–64.

Bruel, W. E. van den (1940).—Un ravageur de l'épinard d'hiver: *Tyroglyphus dimidiatus* Herm. (*longior* Gerv.). *Bull. Inst. Agron. Gembloux* **9**: 81–99.

Buitendijk, A. M. (1945).—Voorloopige catalogus van de acari in de collectie-Oudemans. *Zoöl. Meded.* **24**: 281–391.

Canestrini, G. (1888).—"Prospetto dell' Acarofauna Italiana." Vol. 3. pp. 405–8. (Padua.)

Canestrini, G., and Fanzago, F. (1877).—Intorno agli acari Italiani. *Atti. Ist. Veneto* (5)**4**: 196.

Canestrini, G., and Kramer, P. (1899).—Acarina. Demodicidae und Sarcoptidae. In "Das Tierreich". Vol. 7. pp. 1–193. (Berlin.)

Carter, H. F., and D'Abrera, V. St. E. (1946).—Mites (Acarina)—a probable factor in the aetiology of spasmodic bronchitis and asthma associated with high eosinophilia. *Trans. Roy. Soc. Trop. Med. Hyg.* **39**: 373–87.

Castellani, A. (1912).—Note on copra itch. *J. Trop. Med. Hyg.* **15**: 374.

Cockayne, A. H., and Waters, R. (1916).—The chaff-mite. *N.Z. J. Agric.* **12**: 372–9.

COTTON, R. T., and GOOD, N. E. (1937).—Annotated list of the insects and mites associated with stored grain and cereal products, and of their arthropod parasites and predators. Misc. Publ. U.S. Dep. Agric. No. 258.

DAVIS, A. C. (1944).—The mushroom mite (*Tyrophagus lintneri* (Osborn)) as a pest of cultivated mushrooms. Tech. Bull. U.S. Dep. Agric. No. 879.

DONNADIEU, A. L. (1868).—Recherches anatomiques et zoologiques sur le genre *Trichodactyle*. *Ann. Sci. Nat.* (5)**10**: 69.

DOWLING, G. B., and THOMAS, E. W. P. (1942).—Cheese itch: contact dermatitis due to mite-infested cheese dust. *Brit. Med. J.* **1**(4270): 543.

EALES, N. B. (1918).—Cheese mites. *J. Bd. Agric.* **24**: 1087–96.

EWING, H. E., and NESBITT, H. H. S. (1942).—Some notes on the taxonomy of grain mites (Acarina: Acaridae, formerly Tyroglyphidae). *Proc. Biol. Soc. Wash.* **55**: 121–4.

FINDLAY, W. F. (1921).—Cheese-mite itch and conjunctivitis. *N.Z. J. Hlth. Hosp.* **4**: 57–60.

FUMOUZE, A., and ROBIN, C. (1867).—Mémoire anatomique et zoologique sur les Acariens des genres *Cheyletus*, *Glyciphagus*, et *Tyroglyphus*. *J. Anat., Paris* **4**: 582–5.

GERVAIS, P. (1844).—In "Histoire Naturelle des Insectes." Aptères. (Ed. Walckenaer.) Vol. 3. p. 262.

GHESQUIERE, J. (1947).—Un acarien cosmopolite nouveau pour la faune du Congo belge. *Bull. Cerc. Zool. Congol.* **18**: 52.

GREEN, E. E., and CHINA, W. E. (1943).—"The Generic Names of British Insects." Pt. 8. p. 235. (R. Ent. Soc.: London.)

HEMMING, F. (ED.) (1953).—"Copenhagen Decisions on Zoological Nomenclature." (International Trust for Zoological Nomenclature: London.)

HEMMING, F. (ED.) (1958).—"Opinions and Declarations rendered by the International Commission on Zoological Nomenclature." Vol. 1. Sect. F. Pt. F7. pp. 73–86. Direction 94. (International Trust for Zoological Nomenclature: London.)

HERMANN, J. F. (1804).—"Mémoire Aptérologique." p. 85. pl. 6, fig. 4. (Strasbourg.)

HINMAN, E. H., and KAMPMEIER, R. H. (1934).—Intestinal acariasis due to *Tyroglyphus longior* Gervais. *Amer. J. Trop. Med.* **14**: 355–62.

HIRST, S. (1912).—Report on the mite causing copra itch. *J. Trop. Med. Hyg.* **15**: 374–5.

HIRST, S. (1920).—Species of Arachnida and Myriopoda (scorpions, spiders, mites, ticks and centipedes) injurious to man. Econ. Ser. Brit. Mus. No. 6. 59 pp.

HUGHES, A. M. (1948).—"The Mites Associated with Stored Food Products." Ministry of Agriculture and Fisheries. 168 pp. (H.M.S.O.: London.)

HUGHES, A. M. (1957).—A new species of *Acarus* (*A. gracilis* sp. n.) belonging to the family Tyroglyphidae Donnadieu, 1868 (Acarina). *Ann. Mag. Nat. Hist.* (12) **10**: 753–61.

HULL, J. E. (1931).—Terrestrial Acari of the Tyne Province. IV. Tyroglyphidae. *Trans. North. Nat. Un.* **1**: 37–44.

JARVIS, T. D. (1906).—Mites affecting farm homesteads. *Canad. Ent.* **38**: 239–42.

JARY, S. G. (1937).—A note on *Tyroglyphus longior* var. *castellanii* (Hirst). *J. S.-E. Agric. Coll., Wye* **40**: 130.

JARY, S. G., and STAPLEY, J. H. (1937).—Investigations on the insect and allied pests of cultivated mushrooms. IX. *Tyroglyphus dimidiatus* Herm. (*longior*) Gerv. *J. S.-E. Agric. Coll., Wye* **40**: 119.

JEWSON, S. T., and TATTERSFIELD, F. (1922).—The infestation of fungus cultures by mites (its nature and control together with some remarks on the toxic properties of pyridine). *Ann. Appl. Biol.* **9**: 213–40.

KOCH, C. L. (1841).—"Deutschlands Crustaceen, Miriapoden und Arachniden." Fasc. 32. (Regensburg.)

KOCH, C. L. (1842).—"Vebersicht des Arachnidensystems." Heft 3. (Nürnberg.)

KRANTZ, G. W. (1955).—Some mites injurious to farm-stored grain. *J. Econ. Ent.* **48**: 754–5.

LAPAGE, G. (1945).—Tyroglyphid mites and human disease. *Nature* **156**: 427–8.

LATREILLE, P. A. (1802).—Hist. Nat. Gén. Part. Crust. Ins. Vol. 3. p. 63.

LOMBARDINI, G. (1944).—*Tyroglyphus nadinus* n. sp. *Redia* **30**: 43–69.

MAYER, H. F., and HACK, W. H. (1953).—Redescripcion e investigaciones biologicas sobre *Tyroglyphus longior* Gerv., 1844. (Acarina). *An. Inst. Med. Region., Tucumán* **3**: 283–91.

MAYR, E., LINSLEY, E. G., and USINGER, R. L. (1953).—"Methods and Principles of Systematic Zoology." (McGraw-Hill Book Company, Inc.: New York.)

MÉGNIN, P. (1880).—"Les Parasites et les Maladies Parasitaires." pp. 138–48.

MICHAEL, A. D. (1901, 1903).—"British Tyroglyphidae." Vols. I and II. (Roy. Soc.: London.)

NALEPA, A. (1884–5).—Die Anatomie der Tyroglyphen. *S.B. Akad. Wiss. Wien.* **90** (*Abt.* 1): 197–228.

NEAVE, S. A. (ED.) (1939).—"Nomenclator Zoologicus." Vol. 1. (Zoological Society: London.)

NESBITT, H. H. J. (1945).—A revision of the family Acaridae (Tyroglyphidae), order Acari, based on comparative morphological studies. Pt. 1. Historical, morphological and general taxonomic studies. *Canad. J. Res.* D **23**: 139–88.

NEWSTEAD, R., and MORRIS, H. M. (1920).—Bionomic, morphological, and economic report on the acarids of stored grain and flour. Rep. Grain Pests Comm. Roy. Soc. No. 8. pp. 4–15.

NITZSCH, C. L. (1818).—Allg. Encycl. Wiss. (Eds. Ersch and Gruber.) Vol. 1. pp. 246–52.

NORRIS, D. (1946).—Failure with "DDT" and success with "Gammexane" in the control of the culture mite. *J. Aust. Inst. Agric. Sci.* **12**: 51–2.

OSBORN, H. (1893).—A new mite infecting mushrooms. *Science* **22**: 360.

OUDEMANS, A. C. (1897).—List of Dutch Acari. *Tijdschr. Ent.* **40**: 261–4.

OUDEMANS, A. C. (1906).—"Acari. Nova Guinea. Résultats de l'expédition scientifique Neérlandaise à la Nouvelle-Guinée en 1903, sous les auspices de *Arthur Wichmann*, Chef de l'Expédition." Vol. 5. Book 1. pp. 101–62. (E. J. Brill: Leiden.)

OUDEMANS, A. C. (1916).—Myrmekofile Acari uit Salatiga. *Ent. Ber. Amst.* **4**: 267.

OUDEMANS, A. C. (1923).—Acarologische Aanteekeningen. LXXIII. *Ent. Ber. Amst.* **6**: 201–8.

OUDEMANS, A. C. (1924*a*).—Acarologische Aanteekeningen. LXXIV, LXXV, LXXVI, LXXVII. *Ent. Ber. Amst.* **6**: 249–60, 265–74, 300–10, 317–36.

OUDEMANS, A. C. (1924*b*).—Nieuwste onderzoekingen in de groep der Tyroglyphidae, vulgo kaas-mijten. *Tijdschr. Ent.* **67**: xxii–xxviii.

OUDEMANS, A. C. (1925).—Acarologische Aanteekeningen. LXXIX. *Ent. Ber. Amst.* **7**: 33.

OUDEMANS, A. C. (1926).—Acarologische Aanteekeningen. LXXXIII. *Ent. Ber. Amst.* **7**: 144–7.

OUDEMANS, A. C. (1927).—Acari uit Ambon. *Zoöl. Meded.* **10**: 185–237.

OUDEMANS, A. C. (1929).—"Kritisch Historisch overzicht der Acarologie." II. 1759–1804. *Tijdschr. Ent.* **72** (suppl.).

OUDEMANS, A. C. (1937).—"Kritisch Historisch overzicht der Acarologie." III. 1805–1950. Bd. E. (E. J. Brill: Leiden.)

OUDEMANS, A. C. (1938).—Nieuwe vondsten op het gebied der Systematiek en der Nomenclatuur der Acari. II. *Tijdschr. Ent.* **81**: lxx–lxxx.

OUDEMANS, A. C. (1939).—Neue Funde auf dem Gebiete der Systematik und der Nomenclatur der Acari. VII. *Zool. Anz.* **127**: 184–90.

PAGE, A. B. P., and SHAFIK, M. (1936).—Control of mites on insect-stocks and on fungus cultures by means of fumigation. *Bull. Soc. Ent. Egypte* **20**: 110–43.

RADFORD, C. D. (1950).—Systematic check list of mite genera and type species. *Un. Int. Sci. Biol.* Ser. C. No. 1.

RAINBOW, W. J. (1906).—A synopsis of Australian Acarina. *Rec. Aust. Mus.* **6**: 145–93.

Reuter, E. (1909).—Zur Morphologie und Ontogonie der Acariden. *Acta Soc. Sci. Fenn.* **36**(4): 1–288.

Robertson, P. L. (1946).—Tyroglyphid mites in stored products in New Zealand. *Trans. Roy. Soc. N.Z.* **76**: 185–207.

Robertson, P. L. (1956).—Variation and speciation in *Tyrophagus* (Acarina). Ph.D. Thesis, University of Cambridge.

Sasaki, C. (1921).—A new mite, *Tyroglyphus muscae*, parasitic on the pupae of the silkworm fly. (In Japanese.) *Sangyo Shikenjo Hokoku* **5**: 483–94.

Sasaki, C. (1927).—*Tyroglyphus muscae*, a mite infesting *Sturmia sericariae*, a fly noxious to the silkworm. *J. Coll. Agric., Tokyo* **9**: 151–8.

Schrank, Franz von Paula (1781).—"Enumeratio Insectorum Austriae indiginorum, Augustae Vindelicorum." pp. 507–24.

Seal, W. L., and Eden, W. G. (1956).—Mites in cricket cultures and the toxicities of several acaricides and insecticides to the house cricket. *J. Econ. Ent.* **49**: 262–3.

Solomon, M. E. (1943).—"Tyroglyphid Mites in Stored Products. I. A Survey of Published Information." (H.M.S.O.: London.)

Sorokin, S. V. (1952).—Remarks on the ecology of cereal mites in the nests of ants. (English translation.) *Zool. Zh.* **31**: 544–8.

Sugimoto, M. (1938).—Studies on the Acarina, or mites, of Formosa (2nd Rep.): The tyroglyphid mites and their injuries. II. *J. Taihoku Soc. Agric.* **3**: 42–8.

Sugimoto, M. (1940).—A list of the Formosan Acarina with references. Pt. I. Families Tyroglyphidae and Analgesidae. *Trans. Nat. Hist. Soc. Formosa* **30**: 248–58.

Swan, D. C. (1936).—Berlese's fluid: remarks upon its preparation and use as a mounting medium. *Bull. Ent. Res.* **27**: 389–91.

Turk, F. A. (1953).—A synonymic catalogue of British acari. Pts. I and II. *Ann. Mag. Nat. Hist.* **6**(61): 1–26, **6**(62): 81–99.

Vitzthum, H. (1926).—Malayische Acari. *Treubia* **8**: 1–198.

Vitzthum, H. (1929).—Acari. In "Die Tierwelt Mitteleuropas." Bd. 3. Lieferung 3. (Quelle and Mayer: Leipzig.)

Vitzthum, H. (1940–3).—Acarina. In "Klassen und Ordnungen des Tierreichs." (Ed. H. G. Bronn.) Bd. 5. Abt. IV. Buch 5. (Leipzig.)

Volgin, V. I. (1948).—New species of Acarina of the genus *Tyrophagus* Ouds., 1923 (Tyroglyphidae, Acarina). (In Russian.) *C.R. Acad. Sci. U.R.S.S.* **60**: 509–11.

Volgin, V. I. (1949).—Material relating to the systematics of mites of the genus *Tyrophagus* Ouds., 1923. (In Russian.) *C.R. Acad. Sci. U.R.S.S.* (N.S.) **65**: 385–8.

Volostschuck, V. (1936).—Mites found in stored grain in the Crimea. In Russian, English summary. *Zashch. Rast. Vredit.* **1936**(8): 154–6.

Willcocks, F. C. (1925).—"The Insect and Related Pests of Egypt." II. (Sultanic Agricultural Society: Cairo.)

Womersley, H. (1941).—Studies in Australian Acarina. II. Tyroglyphidae (s.l.). *Rec. S. Aust. Mus.* **6**: 451–88.

Yunker, C. E. (1955).—A proposed classification of the Acaridiae (Acarina: Sarcoptiformes). *Proc. Helminth. Soc. Wash.* **22**: 98–105.

Zakhvatkin, A. A. (1936).—A short key to the granary mites. 2nd Ed. (In Russian.) (Abstr.: *Rev. Appl. Ent.* A **26**: 95.)

Zakhvatkin, A. A. (1941).—Faune de l'U.R.S.S. Arachnoidea. VI. No. 1. Acariens Tyroglyphoides. (In Russian, with keys to genera and species in French.) *Inst. Zool. Acad. Sci. U.R.S.S.* (N.S.) **28**: i–xii, 1–475.

Zimmerman, H. (1918).—Milenbefallene Futtermittel als Ursache von Haustiererkrankungen. *Mitt. dtsch. Landw. Ges.* **33**: 514–18. (Rev.: *Z. angew. Ent.* **6**: 173–4.)

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